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Food Habits of Arborimus albipes, the White-footed Vole, in Oregon[1]

Abstract

Stomach contents and fecal pellets were collected from 21 snap-trapped individuals of *Arborimus albipes*, the white-footed vole. Animals were trapped on the ground surface within a few kilometers of the Oregon Coast. Habitat was the Riparian Alder/Small Stream, *Alnus rubra/Rubus spectabilis* (red alder/salmon berry) union. Fifty-seven percent of the voles' diet came from four hardwood tree species, predominantly *Alnus rubra* and *Salix lasiandra* (red willow), 15 percent from eight shrub species, mainly *Berberis nervosa* (long-leaved Oregon grape) and *Rubus parviflorus* (thimble berry), 23 percent from 15 forbs, primarily *Trifolium repens* (white clover) and *Senecio sylvaticus* (wood grandsel), and small amounts from pteridophytes and grasses. The spatial niche of this vole extends at least from the ground surface into the tree canopy. The diet consists entirely of leaves; no evidence was found of the use of seeds, fruits, fungi, or animal matter. Therefore, the white-footed vole is one of the smallest mammalian browsers known.

Introduction

Nothing has been previously known about the food habits of white-footed voles. Our objectives, therefore, were to identify ingested plant species and to estimate their percentage composition of the voles' diet. The white-footed vole, considered to be one of the rarest microtine rodents north of Mexico, occurs in western Oregon and northwestern California (Maser and Johnson 1967, Johnson and Maser 1982).

Methods and Materials

Stomach contents and fecal pellets were taken from the colon of 21 snap-trapped white-footed voles caught between 1971 and 1973. The stomach contents and fecal pellets were preserved in 70 percent ethanol in glass vials. Trapping sites extended from Bandon, Coos County, to Cascade Head, Tillamook County, approximately 220 km

[1]A contribution of the Oregon Coast Ecological Survey, Puget Sound Museum of Natural History, University of Puget Sound, Tacoma, Washington 98416.

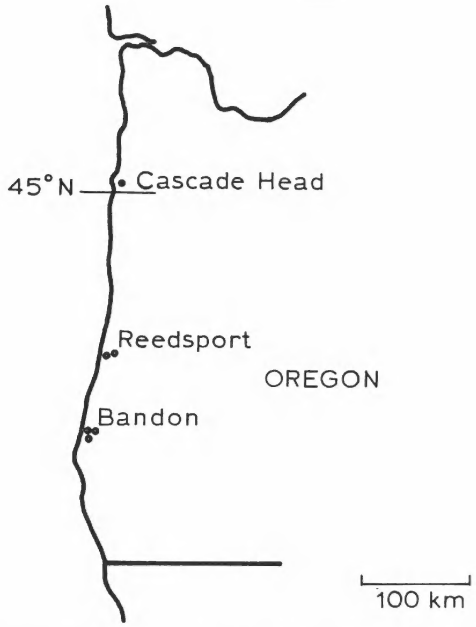

Figure 1. Collecting locations of *Arborimus albipes* represented in samples.

along the Oregon Coast (43°N 124°W to 45°N 124°W) within a few kilometers of the ocean (Fig. 1). Elevations ranged from near sea level to 300 m. Habitat was the Riparian Alder/Small Stream (Maser and Franklin 1974), *Alnus rubra/Rubus spectabilis* (red alder/salmon berry) union.

The voles were caught in February, March, June, July, August, and November. Six random extracts (a total of 36) were removed from the vials for each month of collection. From each of these, approximately 1 mm^3 of stomach or fecal contents was spread on a 25 x 75 mm glass slide, mixed with six drops of glycerol and six drops of chloral hydrate solution, teased, and covered with a 20 x 42 mm glass coverslip. The smear was examined microscopically at x 100 through a wide-field ocular that provided a 2 mm field diameter. Five sweeps of observation were made across a smear with two stops per sweep, for 10 fields per slide. Fragments of ingested material to be identified had to measure at least 0.1 mm in at least one dimension; smaller particles were ignored. Identification of vascular plant species followed a reference collection of black and white photographs of adaxial and abaxial leaf epidermis for more than 50 species likely to be encountered.

Fragment counts were entered on one tally sheet per slide. A sample was defined as that part of the 1 mm^3 pellet or stomach contents appearing in 10 fields examined, or one complete tally sheet. The counts were then tabulated, added, and converted directly into percentage of intake by species. Assumptions about digestive equivalence of leaf epidermis among plant species have been previously challenged (Voth and Black 1973), but since moisture content data were not available for several species encountered, each percentage was allowed to stand as expressed.

Results

Plants identified as intake are given in Table 1. Fragment counts and percentage of fragments for each vascular plant species are shown in Table 2. Thirty plants from 23 families were identified to species in the sample; the species included 2 pteridophytes, 6 trees (2 conifers and 4 hardwoods), 8 shrubs, and 14 forbs. One unidentified grass and 1 unidentified forb (Liliaceae) were also included.

TABLE 1. Vascular plant species found in the diet of **Aborimus albipes.**

Family	Scientific name*	Common name**	Habitat	
			Aquatic	Semi-aquatic Riparian
Equisetaceae	**Equisetum telmataia**	Giant horsetail		"
Polypodiaceae	**Pteridium aquilinum**	Western brake fern		"
Pinaceae	**Tsuga heterophylla**	Western hemlock		"
	Pseudotsuga menziesii	Douglas-fir		"
Gramineae	Unidentified			
Araceae	**Lysichitum americanum**	Yellow skunk cabbage	"	
Liliaceae	**Lilium** or unidentified			
Salicaceae	**Salix lasiandra**	Red willow		"
Betulaceae	**Alnus rubra**	Red alder		"
Urticaceae	**Urtica dioica**	Northwest nettle		"
Portulacaceae	**Montia sibirica**	Western spring beauty		"
Caryophyllaceae	**Arenaria macrophylla**	Long-leaved sandwort		"
Berberidaceae	**Berberis aquifolium**	Oregon grape		"
	Berberis nervosa	Long-leaved Oregon grape		"
Saxifragaceae	**Chrysosplenium glechomaefolium**	Western golden saxifrage	"	..
Rosaceae	**Fragaria vesca**	Western wood strawberry		"
	Rubus parviflorus	Thimble berry		"
	Prunus emarginata	Bitter cherry		"
	Holodiscus discolor	Ocean-spray		"
Leguminosae	**Trifolium repens**	White clover		"
	Lotus crassifolius	Thicket lotus		"
Aceraceae	**Acer circinatum**	Vine maple		"
Violaceae	**Viola glabella**	Smooth woodland violet		"
Umbelliferae	**Oenanthe sarmentosa**	Water parsley	"	..
Ericaceae	**Gaultheria shallon**	Salal		"
	Vaccinium ovatum	Shot huckleberry		"
	Vaccinium parvifolium	Red huckleberry		"
Hydrophyllaceae	**Nemophila parviflora**	Small-flowered nemophila		"
Scrophulariaceae	**Digitalis purpurea**	Foxglove		"
Caprifoliaceae	**Linnaea borealis**	American twinflower		"
	Sambucus cerulea	Blue elderberry		"
Compositae	**Senecio sylvaticus**	Wood groundsel		"

*/Hitchcock 1955

**/Peck 1961

We think 99 percent of all countable fragments (by our definition) were identified and tallied. The remaining "unidentified" species are not shown in a separate category and have been disregarded.

The 18 most abundant species in the diet, including everything that represents at least 1 percent intake, are given in Table 3. Nearly 41 percent of the diet was supplied by one species of hardwood tree, red alder, the dominant tree in the habitat. About 50 percent of the diet was supplied by red alder and red willow (*Salix lasiandra*). Hardwood trees accounted for more than 57 percent of the voles' diet, whereas forbs accounted for more than 23 percent and shrubs for more than 15 percent of the diet. The 18 species most abundant in the diet supplied about 95 percent of the intake. The

TABLE 2. Vascular plant species composition of the diet of **Arborimus albipes.** Systematic according to Hitchcock **et al.** (1955).

Month	Feb.		Mar.		Jun.		Jul.		Aug.		Nov.		Total	
Count & percent of total	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Pteridophytes														
1. **Equisetum telmataia**	1	1											1	0.1
2. **Pteridium aquilinum**							12	10					12	1.7
Spermatophytes														
trees														
conifers, softwoods														
3. **Tsuga heterophylla**			4	4					10	7			14	2.0
4. **Pseudotsuga menziesii**							1	1					1	0.1
anthophytes, hardwoods														
5. **Salix lasiandra**			11	12			32	26	22	14	1	1	66	9.5
6. **Alnus rubra**	28	25	16	17	46	49	54	44	64	42	75	65	283	40.9
7. **Prunus emarginata**	19	17							9	6			28	4.1
8. **Sambucus cerulea**	3	3							5	3	11	10	19	2.8
shrubs														
9. **Berberis aquifolium**			5	5									5	0.7
10. **Berberis nervosa**	36	32			16	17							52	7.5
11. **Rubus parviflorus**	1	1	3	3							16	14	20	2.9
12. **Holodiscus discolor**			1	1					2	1	6	5	9	1.3
13. **Acer circinatum**									1	1			1	0.1
14. **Gaultheria shallon**							5	4					5	0.7
15. **Vaccinium ovatum**			5	5									5	0.7
16. **Vaccinium parvifolium**	1	1							7	5			8	1.2
herbs														
grasses														
17. Unidentified			1	1									1	0.1
forbs														
18. **Lysichitum americanum**			1	1									1	0.1
19. **Urtica dioica**			4	4					3	2			7	1.0
20. **Montia sibirica**									1	1			1	0.1
21. **Arenaria macrophylla**							2	2					2	0.3
22. **Chrysosplenium**														
glechomaefolium							3	2					3	0.4
23. **Fragaria vesca**	2	2	6	6	5	6							13	1.9
24. **Trifolium repens**	10	9	5	5	23	24			2	1			40	5.8
25. **Lotus crassifolius**	3	3			1	1	1	1			3	3	8	1.2
26. **Viola glabella**									1	1			1	0.1
27. **Oenanthe sarmentose**									16	11			16	2.3
28. **Nemophila parviflora**	1	1											1	0.1
29. **Digitalis purpurea**			5	5			1	1			1	1	7	1.0
30. **Linnaea borealis**			22	23			1	1					23	3.3
31. **Senecio sylvaticus**	5	4	6	6	3	3	12	10	9	6	2	2	37	5.4
32. Unidentified	2	2											2	0.3
TOTAL FRAGMENT COUNT	112		95		94		124		152		115		692	
TOTAL PERCENT		101		98		100		102		101		101		99.7

$\frac{692 \text{ fragments}}{360 \text{ fields}} = 19.2/\text{sample} = 1.92/\text{field}$

remaining 14 species comprised less than 1 percent each and a total of only 4 percent of the intake.

The percentage composition of the voles' diet by life forms of the plants, through as much of the calendar year as could be represented, is shown in Figure 2.

Evidence indicates that this small herbivore occupies a spatial niche extending from ground level into the tree canopy, and that its diet consists entirely of leaves from vascular plants. A leaf lamina is chewed into fragments, seldom larger than 0.3 mm in the longest dimension. No seeds, fruits, fungi, or animal parts were found as dietary intake. Some undigested hair shafts and louse instar exoskeletons from groom-

TABLE 3. Rank order of vascular plant species contributing 1 percent or more of the diet of **Arborimus albipes.**

	%
Alnus rubra	40.9
Salix lasiandra	9.5
Berberis nervosa	7.5
Trifolium repens	5.8
Senecio sylvaticus	5.4
Prunus emarginata	4.1
Linnaea borealis	3.3
Rubus parviflorus	2.9
Sambucus cerulea	2.8
Oenanthe sarmentosa	2.3
Tsuga heterophylla	2.0
Fragaria vesca	1.9
Pteridium aquilinum	1.7
Holodiscus discolor	1.3
Vaccinium parvifolium	1.2
Lotus crassifolius	1.2
Urtica dioica	1.0
Digitalis purpurea	1.0
	95.8

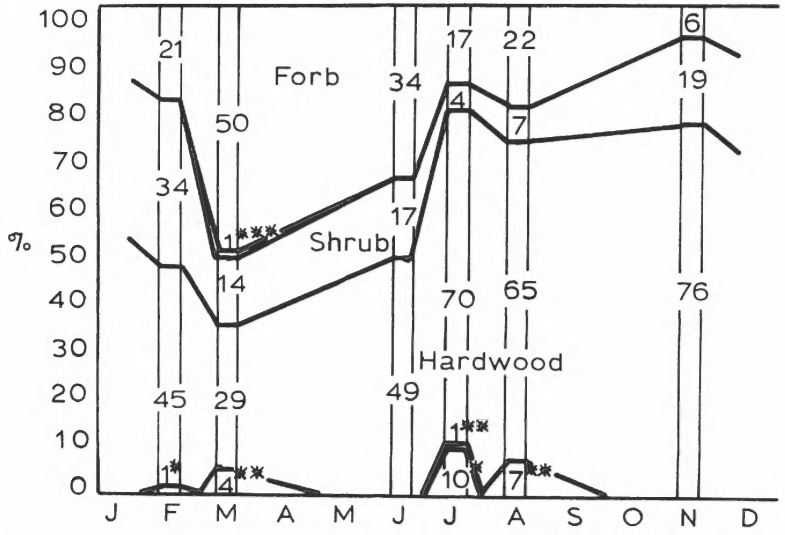

Figure 2. Percentage composition of the diet of *Arborimus albipes* through an annual cycle.
* = Pteridophyte
** = Softwood
*** = Grass

ing were found, however, as were moss gametophytes and pollen grains. The white-footed vole is therefore a browser.

Discussion

Vegetation on the maritime side of the Oregon Coast Range Mountains has been characterized as depauperate in species (Peck 1961, p. 11). Trees dominate, yet few tree species occur. Away from streams and sand dunes of the immediate coast, the climax conifer forest dominants are *Tsuga heterophylla* (western hemlock) and, sometimes

considered subdominant, *Pseudotsuga menziesii* (Douglas-fir). Maritime rain forest precipitation (> 175 cm/year) and the dissection of the landform ensure the development of stream habitats. Hardwoods have long dominated streamsides; first is red alder. Logging of the commercially valuable softwoods has increased hardwood secondary succession, and much land formerly in conifer forest is now covered by red alder. Long history of edge effect has fostered niche proliferation for small mammals in the streamside habitats, despite the paucity of plant species.

Maser and Franklin (1974, p. 29) identified eight habitat types in typical maritime Coast Ranges; the white-footed vole is restricted to type 1—Riparian Alder/Small Stream. Dominant plants of this habitat include the hardwood trees *Alnus rubra* and *Salix lasiandra*; the shrubs *Rubus spectabilis, Rubus parviflorus* (thimble berry), and *Acer circinatum* (vine maple); and the forbs *Urtica dioica* (Northwest nettle), *Oxalis oregana* (Oregon oxalis), and *Linnea borealis* (American twinflower). All have a much larger distribution than the vole.

Maser and Johnson (1967) reviewed the known information about the white-footed vole. Johnson (1973) characterized the genus *Arborimus* (tree voles) as scansorial, arboreal, and the genus *Phenacomys* (heather voles) as cursorial, terrestrial. The tree-climbing ability of the white-footed vole appears to be substantiated by our finding its dependence to be on alder and willow during vernal and pre-abscission seasons. That it can be seen and trapped at ground level, and that it ingests low forbs and grasses, indicate, however, that it certainly is not restricted to the tree canopy.

On logged or burned land, a white-footed vole may be found several hundred meters from a streamside (Maser and Hooven 1969). It also can be found far from water in less disturbed situations (late E. Hooven and M. Lais, pers. comm.). Our results indicate that it depends on riparian or forest rather than on aquatic or semi-aquatic vegetation.

We therefore have found that the habits of *Arborimus albipes* may closely parallel those of *Arborimus longicaudus* (red tree vole). The two voles have a very similar distribution. The spatial niche of *A. longicaudus* extends from ground level into the conifer canopy (Walker 1964, p. 842); the niche of *A. albipes* extends from ground level into the hardwood canopy. Both voles are obligate browsers. This similarity provides significant support for the demonstrated close relationship of the white-footed vole and the red tree vole (Johnson and Maser 1982).

Red tree voles and white-footed voles may be among the smallest browsing arboreal mammals known, close to the minimum size for mammalian herbivores. The wet climate and moderate temperature extremes that contribute to a long growing season and little winterkill, along with limited competition for browse by other mammals in the tree canopy, obviously influence the occurrence of these voles along the coast of Oregon and northwestern California.

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The Anatomy and Histology of the Rudimentary Eye of Neurotrichus

Abstract

Fossorial insectivores are functionally adapted to relative darkness and show anatomical regression in eye morphology. *Scalops* has retained the vitreous body, and the retina has rods and cones. *Talpa* has embryonal lens cells. *Notoryctes*, a fossorial marsupial, has a rudimentary retina without rods and cones, and has lost the vitreous, lens, and pupil. *Neurotrichus* is a rare shrew-like mole with minute optic globes. These are unique in the presence of a pigmented extension of the retina, covering the anterior surface of the optic lens. The globe is collapsed upon the retina and the embryonal lens. Rod and cone cells are poorly defined. The vitreous is missing. There is no palpebral fissure, and the extraocular muscles do not have a proximal bony attachment. The central part of the iris is markedly proliferated. Behavioral studies indicated that *Neurotrichus* is blind, which raises a question about the possible function of the pigmented lenticular covering and the proliferated iris.

Loss of visual perception has occurred in several vertebrate groups, notably in the cave-dwelling fishes and salamanders. In the mammals, two families of the Insectivora (Talpidae, Chrysochloridae) and one family of Marsupalia (Notoryctidae) are of fossorial habit, and have accompanying diminution in visual function. In *Scalops*, Slonaker (1902) demonstrated that despite the rudimentary and presumably non-functional eye, the vitreous is retained in some individual specimens and rods and cones are present. In *Talpa,* another genus of moles, Kohl (1895) and Quilliam (1964) found that the vitreous and aqueous are retained in much the same eye structure as in sighted mammals. Ritter (1899) described in *Talpa* a nearly normal lens structure. Franz (1934) (after Sweet) described *Notoryctes typhlops* in which the vitreous, lens, and pupil are absent, the retina is rudimentary and without rods and cones, and the extraocular muscles are not striated. A comparison of these studies with *Neurotrichus*, a talpid in which the eye structure has not yet been examined, is noteworthy.

Neurotrichus is the smallest of the North American Talpidae, measuring about 100 mm in total length. This talpid is also the least fossorial of the moles, and in its hunting habits on the surface of the forest floor resembles the shrews. *Neurotrichus* is restricted to the humid coastal forests of British Columbia, Washington, Oregon, and Northern California. There is one species (*gibbsii*) and three subspecies (*hyacinthus, gibbsii,* and *minor*). The eye of *Neurotrichus* is subcutaneous and minute. Dalquest and Orcutt (1947) and Reed (1944) have studied *Neurotrichus* in the laboratory and concluded that the animal is blind. This paper describes the ocular anatomy of specimens of *Neurotrichus gibbsii minor* collected at Seattle, Washington.

Methods

Five adult specimens were fixed entire and decalcified. The head was then sectioned sagittally. Twenty adult specimens were dissected and the eyes removed with a block

of epidermis and surrounding tissue. Since the eyes are minute, no intrinsic optic axis could be discovered in specimens fixed in Bouin or Gibson solution. The blocks were sectioned, therefore, at several angles relative to the head. Slides were prepared by paraffin and celloidin block. Sections were stained with haemotoxylneosin, Verhoff, Weigert myelin, Mallory Triple, and Van Gieson. *Neurotrichus* is a rare animal. Few field naturalists have observed it, and no embryological material for sectioning was collected. No EM material has been obtained to date.

Gross Anatomy

There is no palpebral opening. The eye is completely covered by a densely furred integument and is not visible externally except by parting the guard hairs and undercoat. The pigmented globe is then visible through the skin. Directly external to the globe, the skin is hairless and thinner, and thrown into shallow peri-ocular folds. The skin is freely moveable over the eye. When the skin is removed, the eye remains imbedded in the subcuteaneous tissue and is connected, as is the cornea, to the corium by delicate strands of connective tissue.

The eye is a deeply pigmented sphere 0.7 to 1.0 mm in diameter. A thin opaque covering of connective tissue forms a delicate equatorial ring attached to the dermis. No pupil or iris is visible in gross fixed specimens. The extraocular muscles are large at the equatorial ring but rapidly attenuate as they pass posteriorly, close to the course of the optic nerve, to disappear in the subcutaneous tissue over the *M. masseter.* The eye is not contained in a bony orbit but is positioned on the lateral side of the rather conical head at the level of the fourth maxillary tooth. The eye of an embryo specimen (33 mm in total length, head 17 mm) photographed by Dalquest (1947) was deeply pigmented and easily visible through the almost hairless skin.

Histology

Tenon's capsule is thin and cannot be traced anterior to the conjunctival angle. The sclera is composed of several layers of fibroblasts varying from seven to twelve. The cornea is poorly differentiated from the sclera. The cornea is slightly thinner, and the fibroblasts of the substantia propria have more widely separated nuclei. No Bowman's membrane is distinguishable. A few scattered epithelial cells may represent the corneal mesenchymal epithelium.

The choroid is a densely pigmented layer enveloping the globe of the eye except for the small pupillary aperture. At the ciliary body the choroid is much thickened, and here the pars ciliaris retinae separates from it to pass as an adherent pigmented layer across the entire anterior surface of the lens except at the pupil. The non-pigmented cells of this part of the ciliary epithelium, continuous with the neural retinal layer, are cuboidal with eosinophilic cytoplasm. Some of these cells are deflected onto the surface of the lens posterior to the equator, but most form a continuous layer in contact with the anterior capsular cells. The pigmented layer is visible to the pupillary margin.

From the ciliary body the choroid extends anteriorly, closely applied to the inner surface of the sclera and cornea. The choroid is much thickened at the pupil, with light-colored vascular and muscle cells relieving its usually dense pigmentation. There is a well developed pupillary margin. Nearby, in some sections, the pigmented cells of the

anterior surface of the lens are tenuously adherent to the posterior surface of the iris. Otherwise, there is much difficulty trying to distinguish any elements of the pars iridica retinae.

The outer surface of the iris has a one- to two-cell layer of epithelium reflected from the inner surface of the cornea. The entire iris is thick and heavily pigmented.

The ciliary body, composed in the main by the markedly thickened choroid, contains no recognizable muscle cells or fibers of a supensory ligament.

The retina and lens fill the eye. There is no vitreous. The inner limiting membrane is not seen in the section, but most of the remaining retinal layers are clearly demarcated. The optic nerve fibers and ganglion cells are prominent, and nerve fibers loop vertically through this layer. Cells with large nuclei containing a nucleolus and irregular dark-staining bodies in the nucleoplasm and with eosinophilic cytoplasm are present, along with axonic fibers. The inner plexiform layer is present, and a prominent inner nuclear layer is composed of cells with dark nuclei. The nuclear layer is about six cells in depth. There is a prominent outer plexiform layer. The outer nuclear layer is also about six cell layers in depth, the nuclei dark in color. The receptor layer is columnar in structure, but cell detail is faint and definite rods and cones cannot be distinguished. There is a thin outer layer of cells with deeply staining nuclei and pigmented cytoplasm.

The optic nerve can be traced from the optic papilla as it courses posteriorly from the globe to the optic foramen, accompanied by other nerve trunks. Some sections show the optic nerve in close proximity to the ciliary ganglion. The optic nerve penetrates the layers of the globe tangentially. Some fibers can be traced through the entire thickness of the retina as a path of cells entering the ganglion cell layer.

The lens is an ellipsoid structure with a smoothly curved posterior surface and a less smoothly curved anterior surface. The outline of the anterior curvature is modified by the enlarged pupillary rim of the iris. The lens is composed of polyhedral, elongate or columnar cells, each with a dark-staining nucleus. The capsular cells are smaller and flattened. There are numerous vacuoles in the lens substance, especially near the anterior surface.

The posterior chamber of the eye is almost as extensive as the width of the globe, extending from the ciliary bodies across the anterior surface of the lens to the minute pupil. The anterior chamber is all but eliminated by the adherence of the choroid and iris to the inner surface of the sclera and cornea. There is a broad conjunctival sac lined with epithelial cells. These are cuboidal and one- to three-cells thick on the interior surface of the integument, flattened over the cornea, and in thickened layers in the fornices. The conjuctival sac contains desquamated cells and amorphous material. The cells have dark cytoplasm and large oval or rounded, deeply staining nuclei. Some small masses of tubuloalveolar tissue are found adjacent to the conjunctiva, but they open onto the skin surface.

Discussion

The eye of *Neurotrichus* presents comparative anatomists with a unique anatomical feature—i.e., the pigmented covering of the anterior surface of the lens. This pigmented tissue is an exterior layer of the pars ciliaris retinae. No other known vertebrate has taken this evolutionary route. Walls (1943) and Wolff (1949), in their reviews of the comparative anatomy of the vertebrate eye, describe no lenticular pigment layer

comparable to that found in *Neurotrichus*. Of further note in *Neurotrichus* are the markedly proliferated tissue of the central part of the iris, the loss of the vitreous body with collapse of the globe upon the lens and retina, the embryonal structure of the lens, the loss of rods and cones, the loss of any proximal bony attachment of the extra-ocular muscles, and the absence of a palpebral aperture.

The circadian rhythms of rest and activity in *Neurotrichus* are not known. Presumably it maintains a high level of searching and ingestion like the shrews (Sorex and others), with even less dependence on incident light. Its efficient non-visual sensory apparatus allows it to inhabit the dimly lit floor of heavy forests, in and beneath abundant surface vegetation and detritus, where visual acuity is relatively superfluous. Shrews, in similar habitats, have functional eyes. Comparative anatomical and behavioral studies of the microhabitat, which might allow evolutionary discussions, are so far sparse, and a correlation of *Neurotrichus'* peculiar visual anatomy with its adaptive skills can only be conjectural. The moles, more fossorial in habit, show even more anatomical regression in eye structures.

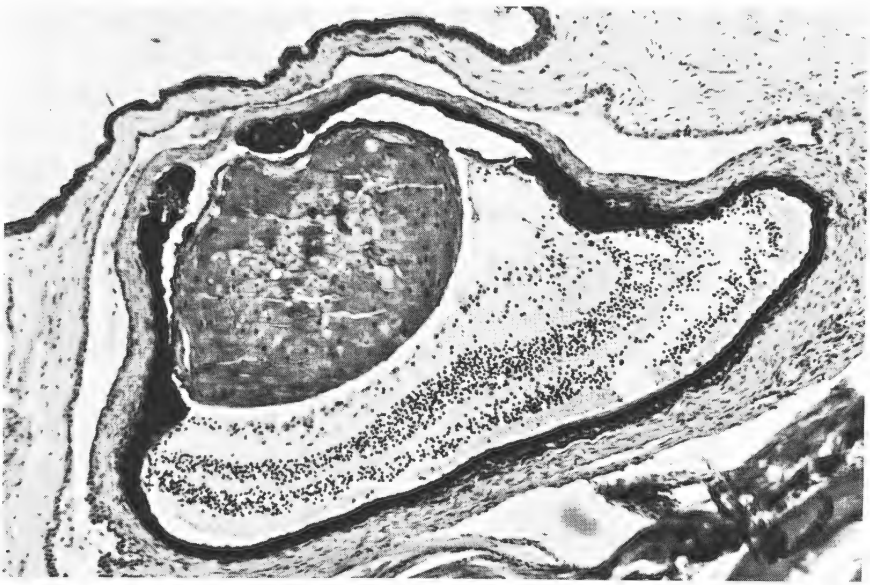

Figure 1. Subcutaneous eye of *Neurotrichus*. Layers of the retina, choroid and sclera, and the lens, iris, pupil, and conjunctival space are visible.

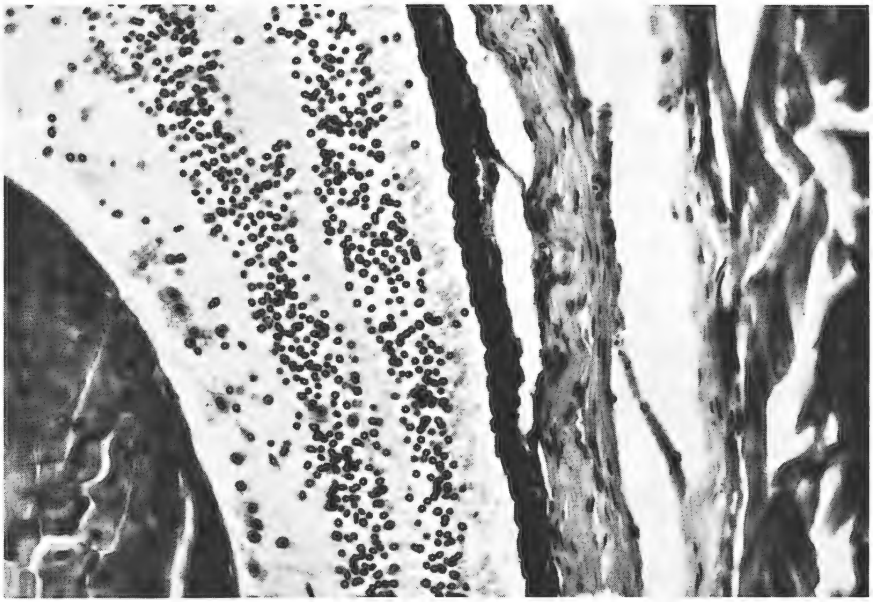

Figure 2. The sclera and pigmented choroid lie to the right of the poorly defined rods and cones.

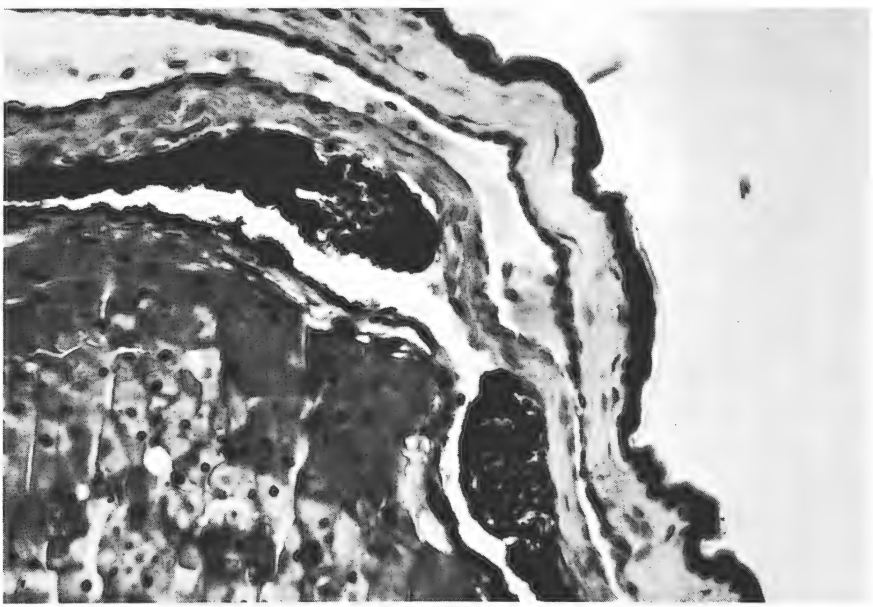

Figure 3. From the right, epidermis, dermis, conjunctival space, cornea-sclera, pupillary margins, posterior chamber, and pigmented pars iridica retinalis.

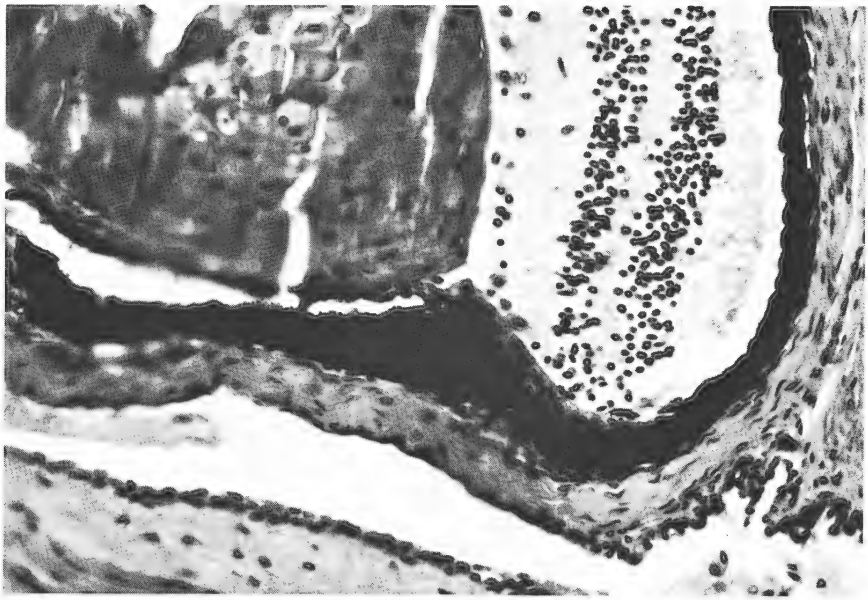

Figure 4. The lens contains cuboidal and elongate cells. The ciliary body (center) lies at the equator of the lens. Anterior to the ciliary body the lens is covered by the pigmented pars iridica retinalis.

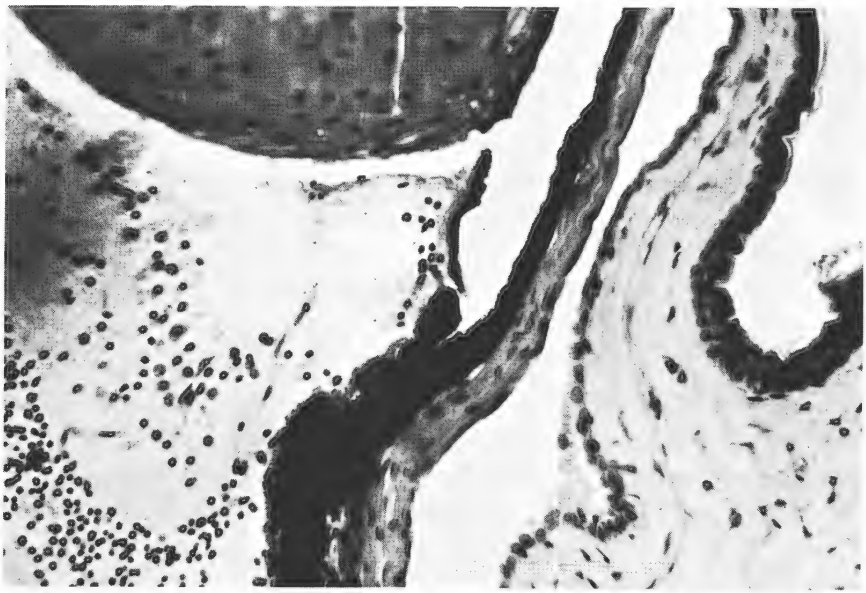

Figure 5. The layers of the retina are to the left. At the ciliary body (center) the continuation of the retina separates from the choroid and passes in front of the lens (top).

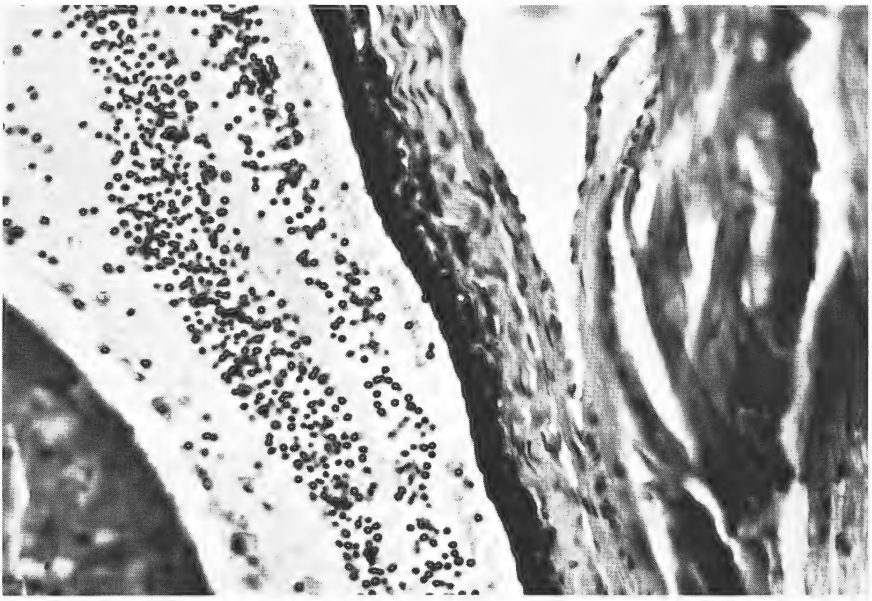

Figure 6. The sclera (center) and the pigmented choroid are external to the poorly defined receptor cells to the left.

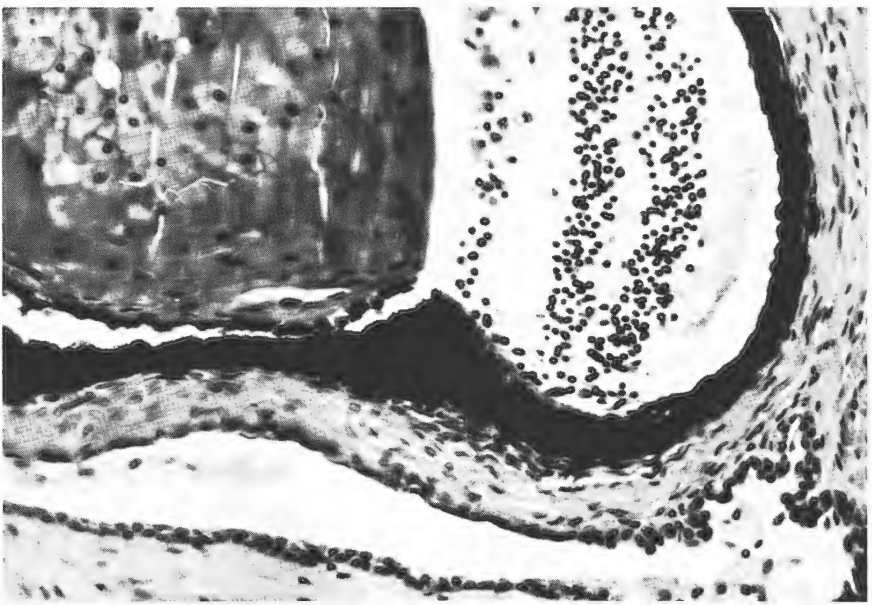

Figure 7. Amorphous receptor cell layer (right).

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Rhodamine B: A Systemic Fluorescent Marker for Studying Mountain Beavers (Aplodontia rufa) and Other Animals

Abstract

Mountain beavers (*Aplodontia rufa*) consuming 15 to 45 mg/kg of Rhodamine B dye developed fluorescent bands in claws within 2 to 4 days and in hair within 5 to 7 days. These bands were invisible in ambient light but appeared orange under ultraviolet light in both live and dead animals. The 1- to 4-mm bands persisted in claws for 6 weeks and in hair for 17 to 28 weeks in free-roaming animals. Bands of dye were also deposited in hair and claws of pocket gophers (*Thomomys mazama*) and in feathers of domestic chickens (*Gallus* sp.) when these animals ingested Rhodamine B dye. The long lasting systemic marking effect should increase the versatility of Rhodamine B in studying mammals and birds.

Introduction

Rhodamine B is an industrial and analytical dye that has been widely used as a marker and tracer in animal studies. This dye is compatible with many organic and inorganic chemicals (Evans and Griffith 1973) and is available from most chemical suppliers. Wildlife uses of Rhodamine B have been mainly for short term marking of the gut, feces, urine, and blood through consumption of dyed bait and through external application of dye solutions for staining hair and feathers. Wadkins (1948), New (1958), Kozlik *et al.* (1959), Gast (1963), Evans and Griffith (1973), and Bruggers and Bortoli (1979) reported on Rhodamine B for studying movement and dispersal of animals; Evans and Griffith (1973), Batcheler and Bell (1974), and Lindsey *et al.* (1979) evaluated its use in animal damage control programs.

During research to evaluate and develop methods for controlling conifer damage caused by mountain beavers (*Aplodontia rufa*), I noted that Rhodamine B, when taken orally by mountain beavers, marked the gall bladder, gut, feces, urine, and oral and urogenital openings and was systemically deposited in the claws and hair. Although systemic action of Rhodamine B dye in animals was noted by Evans and Griffith (1973: 76-77) and by Ellenton and Johnston (1975: 60-67), systemic marking in the claws and hair was not described. This discovery led to concurrent studies on mountain beavers reported herein and on coyotes (*Canis latrans*, Johns and Pan 1981) to study the potential of Rhodamine B as a systemic marker.

Methods and Materials

Commercial Rhodamine B dye (Matheson Coleman and Bell, Manufacturing Chemists, Norwood, Ohio*) was administered in laboratory-held and free-roaming adult and subadult mountain beavers by gavage or by ingestion of fresh apple baits. Laboratory

*Reference to manufacturers or trade names does not imply endorsement by the Federal Government.

held mountain beavers were trapped near Olympia, Washington, held at least seven days, treated, and examined daily until dye marking appeared, then every two weeks thereafter. Field animals were live trapped, weighed, and then treated by gavage or fed apple baits and released at their capture site; they were recaptured and examined at one week and then monthly thereafter.

Test groups of one to five mountain beavers were treated about every two months throughout the year. Twelve caged mountain beavers (5 M, 7 F) were treated by gavage with dosage levels of 5, 15, 25, and 35 mg/kg of body wt.; five field animals (2 M, 3 F) received 30 mg/kg doses. All animals were given single doses of 1.0 to 3.0 ml of a Rhodamine B-water solution; quantities of Rhodamine B in solution were based on individual animal weights to provide consistent mg/kg dosage levels. Ten caged (6 M, 4 F) and four field mountain beavers (1 M, 3 F) were fed apple baits. Thirteen mountain beavers received single treatments, and one animal received two treatments spaced 2 months apart. Baits were prepared by applying Rhodamine B to the surface of apple chunks in concentrations ranging from 0.1 to 0.34 percent (by weight of total bait).

All animals were examined for fluorescent marking in the dark with an ultraviolet (UV) lamp. Gastrointestinal tracts of animals kill-trapped or necropsied during testing were also examined. I used long-wave (366 nm) UV lamps for all examinations.

Blood plasma from four caged mountain beavers treated by gavage with 30 mg/kg doses of Rhodamine B and two untreated control mountain beavers were examined with a Turner Model 111 fluorometer at the Denver Wildlife Research Center. Blood samples ranging from 3 to 4 ml/animal were collected at 1 day, 7 days, and 28 days post treatment. I anesthetized the animals and obtained samples by cardiopuncture using vacutainer tubes containing sodium heparin. The plasma, separated by centrifuging, was initially frozen and then thawed and diluted to 4 cc volume with deionized water for examination.

To evaluate systemic marking on other animals, I treated five adult pocket gophers (*Thomomys mazama*) captured near Olympia, Washington, and six 3- to 5-week-old white, domestic chickens (*Gallus* sp.) by gavage with Rhodamine B. All pocket gophers were treated in September at a 30 mg/kg level, and the chickens (two per treatment level) were treated in May with 5, 15, and 30 mg/kg. Pre- and post-treatment procedures were similar to laboratory-held mountain beavers.

Results

Mountain Beavers

Rhodamine B or a metabolite was internally deposited by systemic action in claws and hair of mountain beavers treated by gavage or by consumption of dyed apple. These bands (Figs. 1 and 2) were invisible in ambient light but fluoresced orange under UV light in both live and dead animals. Claws and hair were marked in all mountain beavers treated by gavage with doses of 15 to 35 mg/kg; the markings of the 5 mg/kg dose were not consistent. Rhodamine B was observed in bands 1- to 4-mm long within 2 to 4 days in claws and in bands 1- to 2-mm long within 5 to 7 days in whiskers and guard hairs. In hair, banding was most evident in the face whiskers and tactile hairs on the forelegs. The dye was present in roots of pulled whiskers within 16 to 40 hours post ingestion; without pulling the hair, the bands were not visible until Day 5.

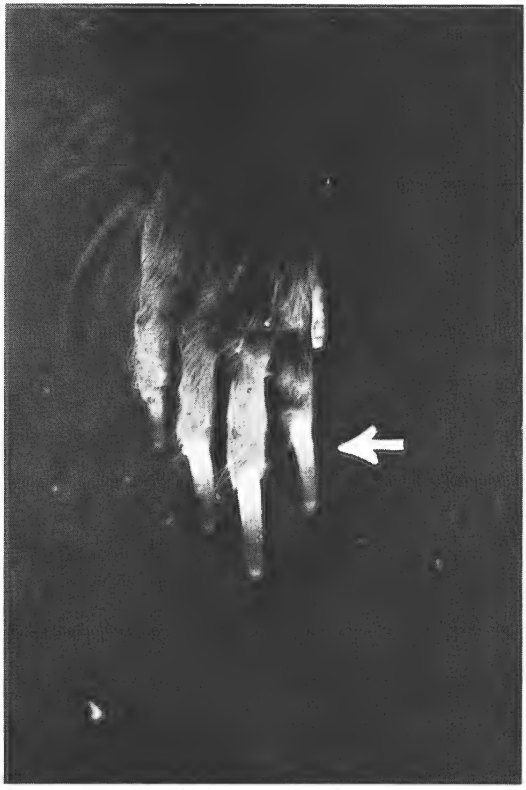

Figure 1. Fluorescent marking in claws of a mountain beaver treated by gavage with Rhodamine B.

Single bands appeared from single treatments and double bands from two treatments spaced 2 months apart. As growth occurred, the bands moved outward and eventually disappeared as hair and claws were worn, broken, or shed.

Mountain beavers readily accepted apple baits coated with Rhodamine B. Consumption of Rhodamine B ranged from 13 to 45 mg/kg. Hair and claws of all mountain beavers were positively marked except for one animal that ingested 13 mg/kg dye. Oral and urogenital areas and front feet of all animals eating dyed apple were visibly stained red for up to 2 weeks. Feces and urine were visibly stained red for 1 to 3 days. Internally, the dye marked the stomach, intestines, and gall bladder. In some animals, the dye diffused through the gall bladder and stained adjacent internal tissue. No adverse physical or behavioral effects from consuming Rhodamine B were observed in laboratory animals.

Duration of banding in caged animals was 19 to 26 weeks in the hair and 13 to 21 weeks in the claws. Duration of hair marking in field animals was 17 to 28 weeks, but the claw marking lasted only 6 weeks because claws were worn away more quickly in free-roaming than in caged animals.

Rhodamine B was detected in blood plasma at 1 day and 7 days but not at 28 days

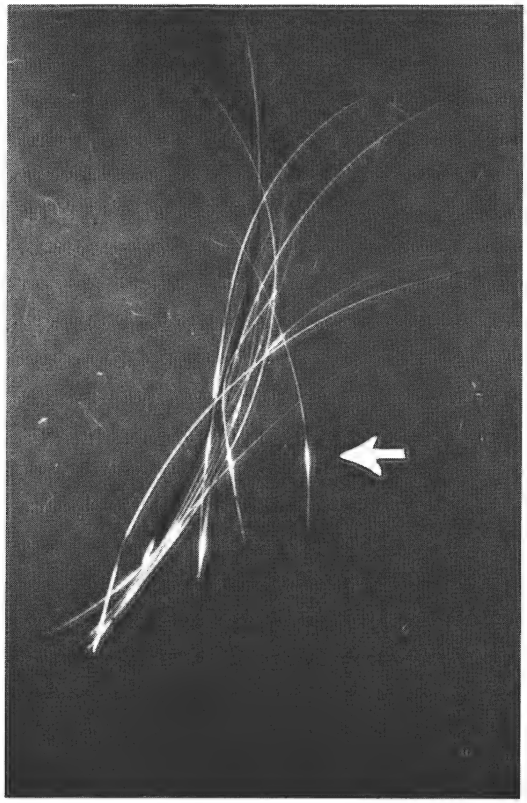

Figure 2. Fluorescent markings in face whiskers removed from a mountain beaver treated by gavage with Rhodamine B.

post ingestion. Rhodamine B was not present in control plasma. Quantitative measurements of Rhodamine B in plasma were not made, but fluorometer data indicate that greatest concentrations of dye were in the 1-day plasma samples.

Pocket Gophers and Chickens

I observed fluorescent bands similar to those described for mountain beavers in whiskers and claws of the five pocket gophers dosed at 30 mg/kg. Bands in whiskers appeared 7 to 15 days post treatment and remained 5 to 6 weeks. Bands in claws appeared 2 to 7 days post treatment and remained 10 weeks. No bands were seen in body hairs.

Domestic chickens developed fluorescent bands in feathers within 24 hours after receiving Rhodamine B. Bands were about 3 mm long and extended the width of the feathers (Fig. 3). Banding was most evident in the primary and secondary wing feathers, but the dye was deposited in all feathers. Banding lasted 1 to 2 weeks in chickens receiving 5 mg/kg Rhodamine B and 15 to 26 weeks in those receiving 15 and 30 mg/kg. The beaks and toenails were not marked.

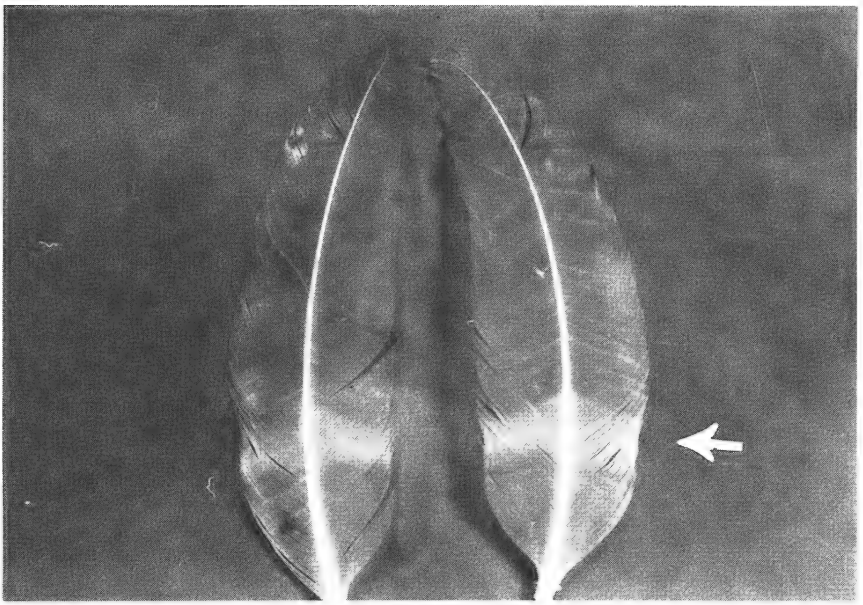

Figure 3. Fluorescent marking in primary feathers of a white domestic chicken treated by gavage with Rhodamine B.

Discussion

Fluorescent banding of claws, hair, and feathers with Rhodamine B expands its already wide application as a marker in animal studies. Because fluorescent bands are transported outward in claws and hair, the rate of growth should reveal when Rhodamine B was ingested. Furthermore, scanning for Rhodamine B does not require necropsy; thus, animals can be retained for further studies. With the use of portable UV lamps, field-trapped animals can be examined and immediately released, reducing stress from capturing and handling. Also, because fluorescent bands are invisible in ambient light, systemic marking should not affect the social structure of birds as noted by Evans and Griffith (1973) when they used an external dye to mark pheasants (*Phasianus colchicus*).

Use of Rhodamine B as a systemic marker may be limited to certain periods of the year in some animals because of the growth characteristics of the hair, claws, and feathers. Johns and Pan (1981) reported that fluorescent banding occurred only in actively growing hair. With animals such as mountain beavers, hair and claws grow continuously, so systemic marking should be effective throughout the year.

The internal "gut" and systemic "hair and claw" marking qualities of Rhodamine B, along with radio telemetry, have allowed us to evaluate methods for controlling mountain beavers and to estimate their exposure to experimental pesticides. Long-term marking gives greater latitude than short-term gut and fecal markers in conducting control and hazard studies. For example, pre- and post-control activity indices or other data can be obtained with less concern that the marker will disappear before animals can be captured for examination.

Rhodamine B, because of its extensive industrial uses, is being investigated for

evidence of carcinogenicity (International Agency for the Research on Cancer 1978, Tomatis *et al.* 1978). Nestmann *et al.* (1979), reported that commercial Rhodamine B dye, but not purified dye, possessed mutagenic activity in *Salmonella* in short term screening tests. Nestmann *et al.* (1979), however, further stated that chemicals showing mutagenic responses in these tests were not necessarily carcinogenic to mammals. Most importantly, Rhodamine B is exempt from legal tolerance requirements in or on raw agricultural commodities (Federal Register 1974). Secondly, no adverse physiological effects from using Rhodamine B for marking wildlife have been reported.

Studies on coyotes (Johns and Pan 1981), plus these on mountain beavers, pocket gophers, and domestic chickens, indicate that systemic hair/claw/feather marking with Rhodamine B is not species specific and should have application to other mammals and birds.

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Modeling the Daily Temperature Cycle

Abstract

A simple model has been developed that can be used to predict the mean daily temperature cycle, by month, provided the mean daily minimum and maximum temperatures are known. Only one set of monthly coefficients is needed for all inland stations in the Pacific Northwest, from Butte, Montana, to Olympia, Washington; but a separate set of coefficients is needed for coastal stations influenced by summer fogs and diurnal land-sea breezes. Tests of the model in predicting mean hourly temperatures at three-hour intervals for all months at seven inland stations yielded a RMSE of 0.96°F (0.6°C) and a maximum absolute error of 3.6°F (2.0°C). Similar tests at two coastal stations yielded a RMSE of 0.35°F (0.2°C), with a maximum absolute error of 1.0°F (0.6°C). The model is based on the equation describing a Pearson type III distribution.

Introduction

Temperature is a primary driving variable in nearly all physical and biological processes —the melting of snow or freezing of water, partitioning of net radiation, plant phenology and growth, and many others. Changing seasonal phenomena may seem self-evident responses to changing temperatures, but the shorter diurnal cycles are not so obvious. Nevertheless, the diurnal cycle may be considered a small scale representation of the annual cycle, and the diurnal range in mean hourly temperatures in a given month may approach the yearly range in mean monthly temperatures.

Physical and biological processes are similarly responsive to these diurnal variations. Snow that is frozen in the morning may be melting in the afternoon. Evapotranspiration may increase by 15-25 percent from morning to afternoon (Gay and Fritschen 1979). McCutchan (1976) cited the need for hourly temperature data for use in a simulation model in forest fire management. These observations indicate the importance of the diurnal temperature cycle in energy exchange and ecosystem processes, particularly in mountainous areas where there are pronounced differences by slope direction and inclination. If we are to be able to model these processes and relate land management responses to specific environments, we must know the daily temperature cycle.

Air temperature is one of the most easily measured of all environmental parameters, yet hourly or continuous temperature data are not readily available in most places.

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Maximum and minimum thermometers are standard instruments in any climatic station, but thermographs that yield hourly or continuous temperature data are usually found only in well equipped first order stations and research facilities.

The lack of data describing the daily temperature cycle has impeded efforts by the senior author to develop estimates of net radiation and its partitioning on mountain slopes. Therefore, we set out in an attempt to develop a simple, general model of the daily temperature cycle that would require only mean minimum and maximum temperature data. This paper presents the results of that effort.

An examination of the literature revealed three basic approaches to the problem of estimating the diurnal temperature cycle: (1) correlation-regression models (Madden and Shea 1978); (2) simple sine curves (Johnson and Fitzpatrick 1977a); and most commonly, (3) reproduction of measured cycles using Fourier series (McCutchan 1976), or a combination of Fourier analysis and sine curves (Johnson and Fitzpatrick 1977b). None seemed fully satisfactory for lack of accuracy, lack of generality, or lack of available data.

Methods

Mean dry bulb air temperature at three hour intervals, by month, were available from 48 climatic stations scattered across two time zones of the Pacific Northwest (Pacific Northwest River Basin Commission 1968). They were gathered over the 10 year period 1949-1958 mostly from airports, but include four mountain passes and two offshore islands in Washington, Oregon, Idaho, and western Montana (Fig. 1).

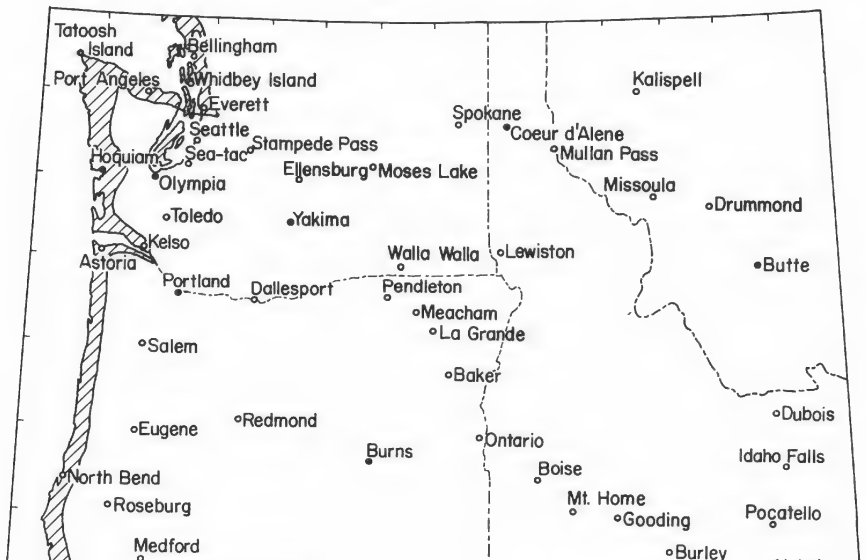

Figure 1. Interior and coastal (hatched) regions of daily temperature cycles. Solid circles indicate stations used for testing model, open circles are stations used as data sources to derive the model.

Normalizing the Data

To reveal whether all stations exhibited a similar temperature pattern, the data from all stations were normalized to the same amplitude and time base to reveal the pure form of the cycle.

Normalization of amplitude was achieved by expressing the temperature at any given time as a decimal fraction of the range. The mean daily instantaneous minimum temperature, by month, was assigned a value of 0, and the corresponding maximum, 1.0. This procedure removed variation in apparent pattern due to widely different diurnal temperature ranges among different months and locations. As the mean instantaneous minimum temperature is always less than the mean three hour minimum (and the maximum greater), the range of the data was increased by 10 percent to correspond with measured instantaneous mean minimums and maximums (Pacific Northwest River Basins Commission 1969). Thus, if the mean three hour minimum temperature was 40°F, and the corresponding maximum 70°F, the range is 30°F and a 10 percent increase of 3°F results in a mean instantaneous minimum of 38.5°F and a maximum of 71.5°F.

In addition to normalizing the temperature amplitude, it was necessary to express all time data in terms of a common time, rather than local time. All clock times were therefore converted to solar time for the appropriate station longitude, using the equation of time (Frank and Lee 1966).

The normalization procedure removed all variability in amplitude and timing in the temperature data except that due to differences in form of the diurnal cycle.

Testing the Data for Uniformity of Form

All data, reduced to a common amplitude and time base, were plotted on graph paper (12 months x 48 stations = 576 curves) to see if they revealed a common form. Visual inspection seemed to confirm a single characteristic shape, resembling a somewhat distorted sine curve for all stations. However, the period of high temperature was broader, and the maximum occurred later during the summer than winter months, as would be expected from the longer period of daylight in summer. Therefore, the curves were segregated by month.

When segregated by month, it became evident that the curves from coastal areas seemed to differ from stations in the interior, exhibiting summer maximums earlier in the day with shorter periods of high temperature. Nine coastal stations exhibiting this pattern were segregated from the rest for separate analysis.

At this stage in the screening process, the data from nine stations were reserved for later use in testing the fit of any model to be developed. The stations, seven from the interior and two from the coast, were selected in a stratified random manner by putting slips with the names of all stations from each group in a single state into a hat and drawing them out. Interior stations reserved were two of eleven from Idaho, one of four from Montana, two of thirteen from Oregon, and two of eleven from Washington. Two of nine coastal stations from Oregon and Washington combined were also reserved. The data from these stations were excluded from those used to develop a model, being reserved to provide independent tests to fit to specific stations.

The remaining data, segregated into interior (32 stations) and coastal (7 stations) sets, were then tested to establish the degree of uniformity of the daily temperature cycle during each month. The population mean and standard deviation of the normal-

ized temperature at each of eight 3-hour intervals throughout the day, for each month, was determined. Only two (of 96 populations) exhibited standard deviations exceeding 0.1 (10 percent) of the mean daily temperature range in each set. From this analysis, we were satisfied that a single model, using the same coefficients, should adequately represent the mean daily temperature cycle for all stations within a given region in any month.

The model remained to be derived, but the goal of a single general model that would be sufficient to describe the mean daily temperature cycle for any station appeared feasible of being met.

Choosing a Model

Inspection revealed that a simple sine curve obviously did not describe the normalized temperature cycle. Trials by Beach (1979) suggested that attempts to develop a model based on Fourier series using only mean monthly minimum and maximum temperature observations were not likely to be fruitful without a heroic number of calculations. For example, McCutchan (1976) required the solution of 30 regression equations to obtain the coefficients for his model from a much stronger data base.

Chapman, observing the fixed upper and lower limits of the normalized curves and the regular seasonal variation in their form, established that a Pearson type III distribution would encompass the range in variation expressed by the data. The Pearson type III model

$$Y = e^{-x\gamma}(1+\tfrac{x}{a})^{\gamma a} \qquad (1)$$

could be modified to yield the temperature at any time, t, provided the coefficients γ, x, and a were known. In modified form to yield temperature:

$$T_t = T_m + T_r\ [e^{-\gamma t}(1+\tfrac{t}{a})^{\gamma a}] \qquad (2)$$

where T = temperature
t = time, hours before or after time of temperature maximum; subject to $t < 0, |t| \leq a$ and $t > 0, |t| \leq 24 - a$.
m = minimum
r = range
a = length of period of rising temperature, hours
γ = an empirically derived coefficient, and
e = base of the natural logarithm (2.718 . . .).

The mean monthly minimum and maximum temperature, and hence the temperature range, are obtained from climatic records of the station of interest. The times of maximum and minimum temperatures were determined by inspection of the mean normalized temperature graph, and the value of the coefficient, "a", determined by subtracting the time of the minimum temperature from the time of the maximum temperature. The value of the coefficient, t, is assigned as the time of interest before (–t) or after (t), the time of maximum temperature. Units involving time were expressed to the nearest 0.1 hours.

The value of the γ coefficients were determined by fitting equation (1) to the mean normalized temperature curve for interior or coastal stations for each month by the method of successive approximation using intervals of 0.01. As the analysis progressed, it soon became apparent that separate values of γ were necessary when $t < 0$ and when $t \geq 0$. The equation is discontinuous at time $t = 24 - a$. A best fit was

accepted when the root mean square deviations of calculated normalized temperature from the observed mean normalized temperature curve for the hours 1, 4, . . . 19, and 22 hours were minimized.

Results

The model of equation (1) fits the mean diurnal normalized temperature curve for all months and both data sets very well. The correlation coefficient between estimated and normalized mean temperature exceeded 0.90 and was significant at or better than the 0.01 probability level in all cases. We had demonstrated that a single, simple model could describe the mean daily temperature cycle for any month for either interior or coastal station data sets. Slightly different coefficients were required to fit interior and coastal patterns. The values of each coefficient for each month and station set are shown in Table 1.

TABLE 1. Coefficients for the equation $T_t = T_m + T_r\,[e^{-\gamma t}(1+\frac{t}{a})^{\gamma a}]$ to estimate temperature in the Pacific Northwest.

	Hr. of maximum T		a (hrs.)		γ, $t < 0$		γ, $t > 0$	
Month	Inland	Coast	Inland	Coast	Inland	Coast	Inland	Coast
Jan	13.5	13.2	7.2	7.2	0.50	0.62	0.55	0.65
Feb	14.3	14.0	8.0	8.0	0.37	0.40	0.62	0.68
Mar	14.5	14.2	8.6	8.3	0.28	0.28	0.60	0.65
Apr	14.7	14.2	9.9	9.4	0.20	0.20	0.62	0.72
May	14.7	14.2	10.4	10.2	0.20	0.20	0.62	0.72
Jun	14.8	14.2	11.0	10.7	0.20	0.22	0.62	0.72
Jul	15.0	14.2	11.3	10.6	0.22	0.24	0.68	0.70
Aug	14.7	14.2	10.4	9.8	0.24	0.24	0.60	0.75
Sep	14.5	14.2	9.4	9.0	0.23	0.20	0.64	0.78
Oct	14.1	13.8	8.5	8.2	0.24	0.24	0.74	0.82
Nov	13.6	13.2	7.8	7.6	0.36	0.42	0.66	0.78
Dec	13.5	13.0	7.2	7.2	0.48	0.60	0.66	0.66

It is one thing to force fit a model to the mean curves from which the coefficients of the model were derived, but it remained to be seen whether the model and the same coefficients could be used to reproduce the mean daily temperature curve, by month, for individual stations independent of those used to derive them. Accordingly, the model of equation (2) using the coefficients of Table 1 was used to predict mean dry bulb temperatures at three hour intervals (1, 4, . . . 22 hours), by month, at each of the nine stations reserved for independent tests of the model.

The independent tests demonstrate an accurate fit of estimated to actual temperature for all months and all stations. The maximum deviation found for all 864 station-hour-months was 3.6°F (2°C) at Portland, Oregon, at 10 a.m. in July, and the maximum root mean square deviation of the eight hourly estimates of the mean daily cycle was 1.83°F (1°C) for Burns, Oregon, in July, when the observed mean daily temperature amplitude was 35.9° (20°C). Table 2 shows the statistical data of degree of fit for each station month used in this independent test. The data for five selected months for the station with the poorest hourly fit (Portland, Oregon) and the best overall fit (Coeur d'Alene, Idaho) are presented in Figures 2 and 3. When all test data for the inland stations were combined (8 hours x 12 months x 7 stations = 672 station-hour-months), the root mean squared error (RMSE) in estimated temperature was 0.96°F

TABLE 2. Statistics of fit of estimated to measured mean temperatures from nine stations, for 8 hrs. each day.

Station	Month	RMSE(°F)	Max. absolute error(°F)	r^2
Interior				
Coeur d'Alene, Idaho	1	0.27	0.5	.9929
	2	0.24	0.4	.9967
	3	0.43	0.9	.9946
	4	0.45	0.8	.9744
	5	0.67	1.2	.9911
	6	0.67	1.0	.9910
	7	1.04	1.6	.9880
	8	1.00	2.0	.9873
	9	0.90	1.7	.9893
	10	0.59	1.3	.9931
	11	0.53	1.1	.9811
	12	0.30	0.5	.9807
	yr.	0.65	2.0	.9984
Malad City, Idaho	1	0.79	1.7	.9783
	2	0.77	1.4	.9857
	3	0.97	1.6	.9768
	4	1.38	2.4	.9775
	5	1.69	3.3	.9665
	6	1.45	2.9	.9832
	7	1.41	2.5	.9860
	8	1.74	2.5	.9800
	9	1.77	2.7	.9804
	10	1.02	1.6	.9938
	11	1.13	1.8	.9813
	12	0.94	2.0	.9615
	yr.	1.30	3.3	.9954
Butte, Montana	1	0.83	1.1	.9803
	2	0.56	1.0	.9963
	3	0.74	1.4	.9879
	4	0.51	1.0	.9976
	5	0.88	1.8	.9885
	6	0.66	1.4	.9946
	7	1.37	2.1	.9923
	8	1.17	1.8	.9897
	9	0.51	0.8	.9978
	10	0.77	1.6	.9957
	11	0.86	1.4	.9933
	12	1.06	1.7	.9852
	yr.	0.87	2.1	.9981
Burns, Oregon	1	1.19	2.0	.9613
	2	1.19	2.0	.9819
	3	0.44	0.7	.9954
	4	0.71	1.2	.9936
	5	0.73	1.0	.9926
	6	1.02	1.8	.9900
	7	1.83	2.5	.9752
	8	1.37	2.9	.9822
	9	1.73	3.4	.9737
	10	1.69	3.2	.9742
	11	1.04	2.1	.9856
	12	1.08	1.8	.9742
	yr.	1.24	3.4	.9951
Portland, Oregon	1	0.36	0.6	.9776
	2	0.36	0.7	.9921
	3	0.50	0.8	.9956
	4	0.78	1.8	.9883
	5	0.82	1.9	.9894
	6	0.91	2.1	.9873
	7	1.73	3.6	.9640

TABLE 2. (Continued)

	8	1.39	3.4	.9747
	9	0.95	2.2	.9854
	10	0.63	1.3	.9929
	11	0.46	0.7	.9901
	12	0.34	0.7	.9854
	yr.	0.88	3.6	.9959
Olympia, Washington	1	0.34	0.5	.9861
	2	0.26	0.5	.9956
	3	0.30	0.6	.9980
	4	0.27	0.4	.9995
	5	0.62	1.0	.9941
	6	0.73	1.4	.9918
	7	1.12	2.2	.9894
	8	0.83	1.5	.9941
	9	0.47	0.8	.9975
	10	0.32	0.5	.9971
	11	0.39	0.6	.9908
	12	0.30	0.5	.9899
	yr.	0.56	2.2	.9982
Yakima, Washington	1	0.51	0.8	.9904
	2	0.62	1.0	.9873
	3	0.86	1.6	.9872
	4	0.86	1.9	.9941
	5	1.14	2.9	.9861
	6	0.75	2.0	.9936
	7	1.27	2.6	.9937
	8	1.30	2.5	.9884
	9	1.42	2.4	.9829
	10	1.09	1.9	.9865
	11	0.52	0.9	.9927
	12	0.52	0.8	.9911
	yr.	0.96	2.9	.9971
Coastal				
Hoquiam, Washington	1	0.26	0.4	.9912
	2	0.32	0.5	.9896
	3	0.38	0.8	.9976
	4	0.50	0.9	.9930
	5	0.50	1.0	.9914
	6	0.34	0.6	.9947
	7	0.33	0.5	.9973
	8	0.50	0.8	.9702
	9	0.49	1.0	.9946
	10	0.45	0.9	.9965
	11	0.55	0.9	.9841
	12	0.17	0.3	.9960
	yr.	0.42	1.0	.9979
Tatoosh Is., Washington	1	0.28	0.4	.9156
	2	0.29	0.4	.9430
	3	0.22	0.4	.9857
	4	0.35	0.7	.9674
	5	0.17	0.4	.9905
	6	0.25	0.5	.9898
	7	0.19	0.3	.9889
	8	0.26	0.4	.9806
	9	0.30	0.5	.9749
	10	0.33	0.7	.9689
	11	0.21	0.3	.9558
	12	0.12	0.2	.9638
	yr.	0.25	0.7	.9979

(0.6°C), and the maximum absolute error was 3.6°F (2.0°C). Coastal station combined tests ($n = 192$ station-hour-months) yielded a RMSE of 0.35°F (0.2°C), and a maximum absolute error of 1.0°F (0.6°C).

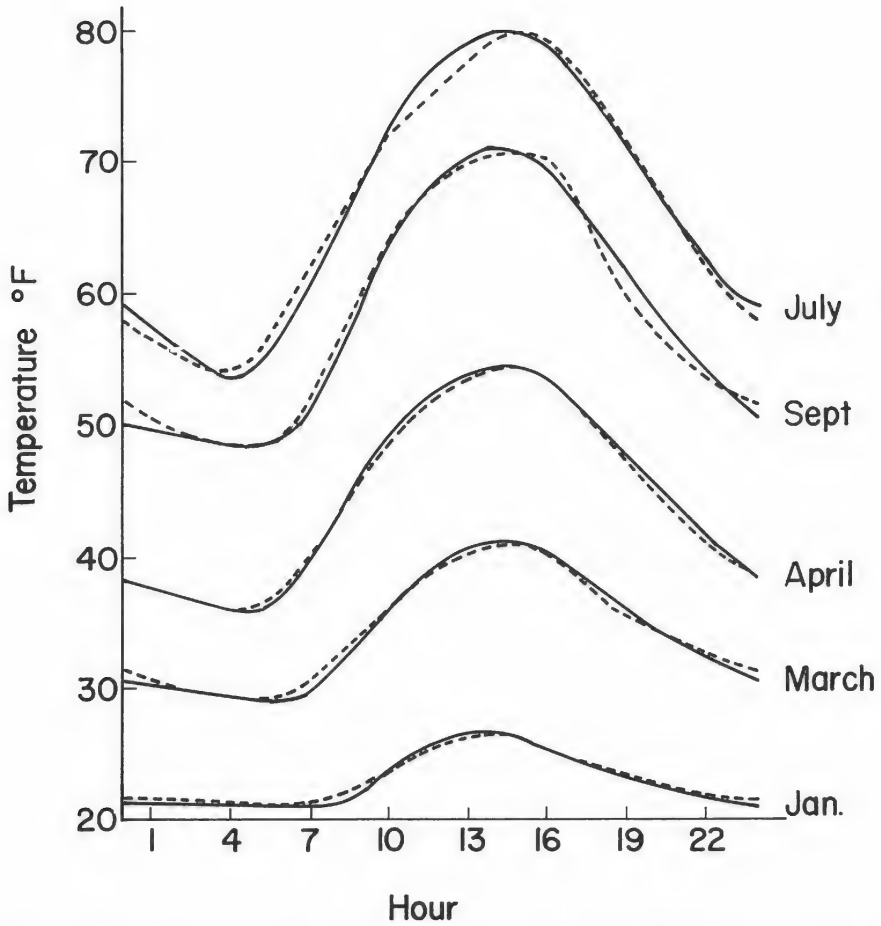

Figure 2. Estimated (solid line) and measured (broken line) mean daily temperature cycle for selected months, Coeur d'Alene, Idaho.

Discussion and Conclusions

The simple model, based on the Pearson type III distribution, can be used to accurately estimate the mean daily temperature cycle, by month, for climatic stations in the Pacific Northwest, provided that the mean daily maximum and minimum temperatures are known. The same monthly coefficients are used for all inland stations, from Butte, Montana to Olympia, Washington—desert, forest, or mountain pass; but a separate set of coefficients is needed for coastal stations influenced by diurnal land-sea breezes and summer morning fog and clouds (Fig. 3).

The region around southern Puget Sound and the lower Columbia River appears to exhibit characteristics of a transition zone, particularly in summer, although stations in these areas exhibit more of the characteristics of interior stations than of coastal stations. Nevertheless, examination of cloud cover data (Pacific Northwest River Basins

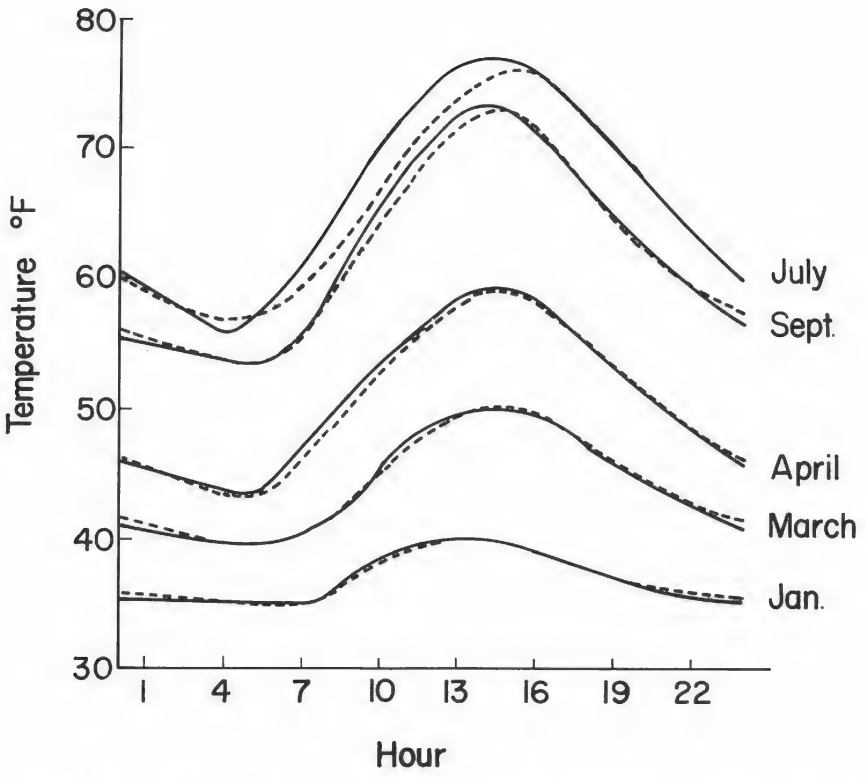

Figure 3. Estimated (solid line) and measured (broken line) mean daily temperature cycle for selected months, Portland, Oregon.

Commission 1968), suggested that the large deviations of estimated from observed temperatures in the morning in summer for Portland, Oregon, were a result of the greater morning cloudiness at that station. Predicted temperatures consistently exceeded observed temperatures, which is what would be expected if greater cloudiness delayed surface heating in the morning. A similar, but less pronounced, effect also occurs at Olympia, Washington.

The model and coefficients presented herein should be applicable for estimating the mean temperature at any given hour, by month, at most stations in the Pacific Northwest. There may be some risk in applying the model to stations located in frost pockets or other areas of poor nocturnal air drainage that might be expected to distort the normal daily temperature pattern.

Coefficients should probably be developed separately if the model is applied outside the region in which it was developed. The coefficients are clearly sensitive to daylength and probably to different diurnal patterns and amounts of cloudiness.

Finally, the model should not be used to predict the temperature pattern for any specific day.

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Small Mammal Populations and Food Selection in Relation to Timber Harvest Practices in the Western Cascade Mountains

Abstract

Small mammals were snap-trapped in a mature conifer forest, unburned clearcuts, and burned clearcut in the western Cascade Mountains in central Washington. The largest populations were in unburned clearcuts, and the smallest overall population was in the forest. *Sorex trowbridgii* was the most abundant insectivore caught. *Clethrionomys gapperi* was the most abundant rodent caught in most clearcuts, and its population was the largest of any species in the study area. Other species caught include *Sorex monticolus, Neurotrichus gibbsii, Eutamias townsendii, Glaucomys sabrinus, Peromyscus maniculatus, Microtus townsendii,* and *Zapus trinotatus.* Vegetation and percent cover were analyzed in the study area, and small mammal stomach contents of all nine animal species were examined. In the forest and burned clearcut, small mammals ate more invertebrates than any other food type. In unburned clearcuts, fungi and epiphytic lichens, especially *Alectoria sarmentosa,* and conifer seeds were the major foods eaten by rodents.

Introduction

In contiguous forests, cover is an important factor limiting small mammal presence and relative abundance (Dice 1931; Getz 1970; Miller and Getz 1972, 1973, 1977; Dragavon 1978). Logging and controlled burns drastically alter vegetation, ground cover, and soil moisture. Small mammal species react differently to habitat alterations depending on their specific shelter, energy, nutrient, and moisture requirements (Bunnell and Eastman 1976).

Most studies relating small mammal species distribution and abundance in forests have shown a decline in forest dwelling small mammals and an increase in small mammals typical of grassland plant communities wherever forests are logged and burned (Gashwiler 1959, 1970; Ahlgren 1966; Miller and Getz 1972, 1973, 1977; Sims and Buckner 1973; Hooven and Black 1976). These studies were conducted in areas with a low percentage of ground cover and ranged over a period of several years after clearcutting. Other studies (Kirtland 1977, Martell and Radvanyi 1977) found that after spruce forests were clearcut, small mammals increased within the first year after logging and then decreased in subsequent years. Ground cover estimates were not given in these studies.

The purpose of this study was to examine the relative abundance of small mammals in a mature western hemlock (*Tsuga heterophylla*) forest, recent clearcuts, and burned

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clearcut. The clearcuts were characterized by a large amount of slash, such that the total amount of ground cover in the clearcuts was greater than in the forest. In addition, small mammal food habits, which were related to vegetation abundance, were compared among species and within a single species in different habitats. Small mammal sampling was conducted only during July and September 1980, approximately three months after the forest was logged and two months after the logged area was burned. Although we realize the intersite variation and seasonal fluctuation known for small mammal abundance and food selection, we believe that this study is of merit because of the direct correlations we found among mammal abundance, food selection, and debris and vegetative cover.

Description

Our study area is located on the west slope of the Cascade mountains in central Washington within the Mt. Baker-Snoqualmie National Forest. Annual precipitation in the general area averages 229 cm.; elevation in the study area ranges from 853 m to 1058 m. The area has a northwest exposure and a 66 percent slope which decreases to 33 percent in the western one-third section. Western redcedar (*Thuja plicata*), western hemlock, Douglas-fir (*Pseudotsuga menziesii*), and silver fir (*Abies amabilis*) are the major tree species. These stands are about 110 years old, with a stocking of about 385 trees per ha (Fig. 1). Part of the forest was logged during fall 1979 and spring 1980 in six clearcut units. Our study area includes part of the remaining mature forest and three clearcuts that are closest to the mature forest. They are 12 ha, 25 ha, and 8.5 ha in size. Strips of mature conifers (61 m-120 m wide) are left between the clearcuts (Fig. 2). A logging road crosses the eastern section of the clearcuts. A commercial mixture of grass and clover was planted in 4 m to 9 m strips on either side of the logging road to minimize erosion. The soil is relatively moist, rocky, and acidic. Ground water seepage and permanent streams occur throughout the study area. The three clearcuts are referred to as Clearcut 1, 2, and 3. Clearcut 2, which was burned in late July 1980, is referred to as burned Clearcut 2.

Methods

Vegetation was sampled by establishing five random subplots within the forest and each clearcut. Each subplot encompassed an area of 9.37 m. The vascular vegetation within each subplot was recorded and rated as either abundant, common, or occasional. Vegetation was classified into three vertical categories: overstory tree/shrub stratum greater than 4 m, understory tree/shrub stratum less than 4 m, and herbaceus stratum. Percent vegetative cover and down material was recorded. Scientific names of plants follow Hale (1969) and Hitchcock and Cronquist (1973).

Reference plant material was collected in the forest and clearcuts, and permanent plant slides for identification of food items in dietary analysis were prepared (see Baumgartner and Marten 1939).

Five 90 x 100 m trapping grids, each composed of 110 stations (10 x 11 lines) with 10 m spacing between stations, were established in the forest and clearcuts. Grids were located a minimum of 30 m from a road or sample plot edge. Two Museum Special snap traps, baited with peanut butter and rolled wheat, were placed within a

Figure 1. Mature forest in the study area.

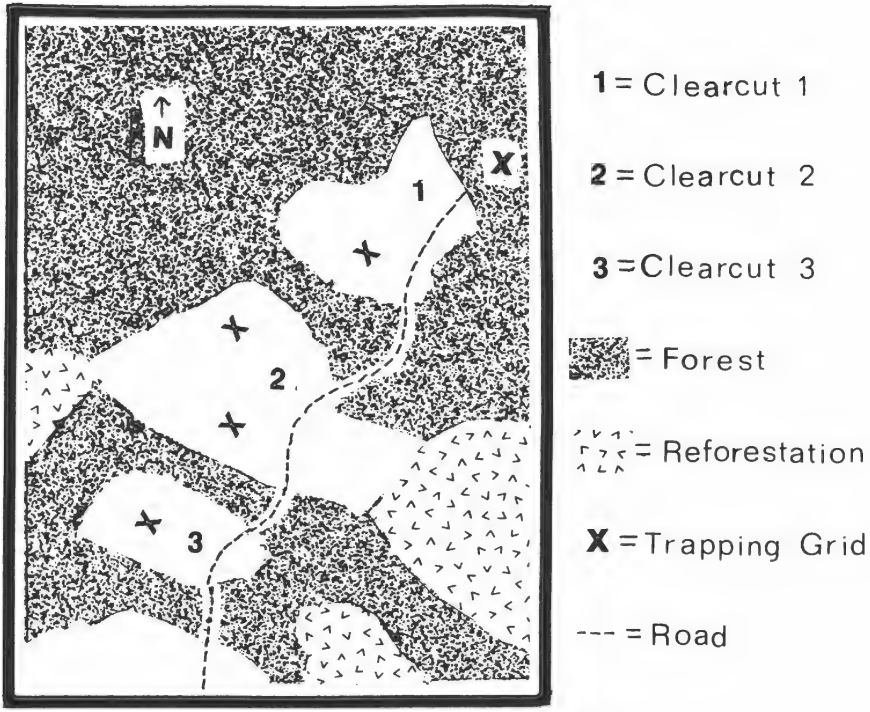

Figure 2. Topographic outline of study area.

one-meter radius of each station. Four similarly baited snap rat traps were placed at intermittent stations within each line (44 traps/grid). Forest traps were additionally baited with apple slices to sample the northern flying squirrel (*Glaucomys sabrinus*) population.

Traps were set on four consecutive nights, totaling 1056 trap night in each sample plot. Clearcuts 1 and 2 were sampled during 11-14 July, the forest sampled 15-18 September, and Clearcut 3 and burned Clearcut 2 sampled 22-25 September 1980. The two grids in Clearcut 2 were placed in opposite corners of the plot (Fig. 2) and were sampled at different dates. Small mammal specimens were collected daily and subsequently prepared as study specimens and deposited at the Washington State Museum, University of Washington, Seattle. Scientific names follow Hall and Kelson (1959) and Hennings and Hoffman (1977).

Standard weights and measurements as well as sex and reproductive status were obtained from all specimens. Stomach contents were preserved in 12 percent formalin. Stomach content fragments were identified using 100 power compound microscopes. Cellular characteristics of the stomach plant fragments were compared to plant reference slides. Invertebrates were noted and tallied but were not identified as to species. Identified plant and animal fragments from stomachs were divided into six categories: 1) fungi and lichen, 2) conifer seed parts, 3) shrub, herbaceous leaf and reproductive parts, 4) grass leaves and seed parts, 5) invertebrate parts, and 6) other matter.

Frequency of occurrence of fragments in these categories was determined by examining 20 randomly selected microscopic fields within each stomach's contents and identifying the fragment closest to the microscope pointer. This information was pooled across animals to obtain relative frequency estimates for each habitat.

Results and Discussion

Vegetation

The major plant species and their relative abundance within each vertical stratum in the forest, clearcuts, and burned Clearcut 2 are listed in Table 1. Dominant shrubs in the forest and clearcuts were salal (*Gaultheria shallon*) and huckleberry (*Vaccinium ovalifolium*). The most aboundant herbaceous plant in the forest was twinflower (*Linnaea borealis*). The percent overstory canopy cover and understory ground cover is listed in Table 2. Total ground cover in thhe clearcuts ranged from 83 to 90 percent (Fig. 3),

TABLE 1. Relative abundance of major plant species.

Species	Forest	Clearcut 1	Clearcut 2	Burned Clearcut 2	Clearcut 3
Overstory tree stratum					
Abies amabalis	O[1]	O		O	O
Pseudotsuga menziesii	C[2]	O	O	O	O
Thuja plicata	A[3]	O	O	O	O
Tsuga heterophylla	A	O	O		O
Understory tree/shrub stratum					
Abies amabilis	O		O		O
Berberis nervosa	O	C	C	O	C
Gaultheria shallon	A	A	A	O	A
Holodiscus discolor		O	O		
Meziesia ferrugina	C	C	C	O	A
Oplopanax horridum		O	O	O	
Pseudotsuga menziesii	O	O			O
Rosa gymnocarpa	O				
Thuja plicata	O	O			O
Tsuga heterophylla	C	O	O		O
Vaccinium ovalifolium	A	A	A	C	C
Herbaceous stratum					
Blechnum spicant	O		C	C	C
Caltha biflora	O	O	O	O	O
Chimaphila menziesii	C	O	O		O
Clintonia uniflora	O	C	O	O	O
Corallorhiza mertensiana	C				
Cornus canadensis	C	C	C	C	C
Galium trifidum			O		O
Gymnocarpium dryopteris	O				
Linnaea borealis	A				
Montia sibirica			O		
Pyrola secunda	O	O	O		O
Streptopus roseus		O	O		
Tiarella trifoliata	O	O	C	O	C
Festuca sp.	O				
Commercial mix of grass and clover (Agrostis, Bromus, Festuca, Phleum, Trifolium)		O	O	O	O

Overstory tree stratum

[1]O = Occasional

[2]C = Common

[3]A = Abundant

TABLE 2. Percent overstory canopy cover and understory ground cover on the sample plots. T= Trace.

	Forest	Clearcut 1	Clearcut 2	Burned Clearcut 2	Clearcut 3
Overstory canopy cover	65	T	T	T	T
Understory herb and shrub cover	40	21	22	8	30
Dead and down material	10	62	64	45	60
Total ground cover	50	83	86	53	90

Figure 3. Slash and vegetation remaining on clearcuts after logging.

and the forest averaged 50 percent. The amount of down material left on the clearcuts ranged from 252-296 tons per ha.

On 20 July 1980, Clearcut 2 was burned to remove excess slash. The moderately intense slash burn fire on Clearcut 2 consumed 42 percent of the total slash volume. The fire removed small slash and most of the ground cover. Large logs and stumps were only charred by the fire. The average fuel depth was reduced from 76 cm before the burn to 46 cm. After the fire about 108 tons/ha of down material remained. Live vegetation following the burn was composed primarily of deerfern (*Blechnum spicant*), bunchberry (*Cornus canadensis*), and huckleberry (Fig. 4).

Small Mammal Abundance

The total number of small mammals caught in the mature forest, clearcuts, and burned Clearcut 2 are listed in Table 3. The forest and burned clearcuts had fewer small mammals than unburned clearcuts. The most frequently caught small mammals in the forest—Trowbridge shrews (*Sorex trowbridgii*), deer mice (*Peromyscus maniculatus*), and

Figure 4. Remaining slash and vegetation following a prescribed burn on Clearcut 2.

TABLE 3. Number of small mammals caught in the study area.

Species	Forest	Clearcut 1	Clearcut 2	Burned Clearcut 2	Clearcut 3	Total
Sorex monticolus	4	10	8	4		26
Sorex trowbridgii	6	4	21	15	30	76
Neurotrichus gibbsii		1	3	3	1	8
Eutamias townsendii	1	2	6	2		11
Glaucomys sabrinus	1					1
Peromyscus maniculatus	7	22	24	1	17	71
Clethrionomys gapperi	6	33	23	7	45	114
Microtus townsendii				3	4	7
Zaus trinotatus			3			3
Total	25	72	88	35	97	317

red-backed voles (*Clethrionomys gapperi*)—were also the most abundant small mammals in the clearcuts. Two species which are typical of grassland plant communities, Townsend voles (*Microtus townsendii*) and Pacific jumping mice (*Zapus trinotatus*), were not found in the forest but were present in clearcuts.

In the forest no one small mammal species predominated. In most clearcuts the red-backed vole was the most abundant species, and its total population was the largest in the study area. Townsend voles were caught in Clearcut 3 and burned Clearcut 2 only in September. The three jumping mice caught in Clearcut 2 during July were caught in the same trap on different trap nights. In burned Clearcut 2, there were at least twice as many Trowbridge shrews caught than any other small mammal species. Only

one deer mouse was caught in burned Clearcut 2, compared to 17 caught in Clearcut 3, which was also sampled during September.

As the red-backed vole catch increased in two clearcuts, fewer deer mice were caught. Clearcut 3 had fewer deer mice and more red-backed voles than any other clearcut. On the basis of reproductive condition, total length, and body weight, we found that 61 percent of the deer mice and 33 percent of the red-back voles caught in July were immatures. In Clearcut 3, trapped in September, we found that 13 percent of the deer mice and 71 percent of the red-backed voles were immatures. The increase in voles and lack of increase in deer mice in September may be explained by the number of immatures of each species entering the population.

Small Mammal Stomach Contents

Fungi and lichens were the major foods eaten by most rodents, particularly red-backed voles, in clearcuts (Table 4). Epiphytic lichens, hair moss (*Alectoria sarmentosa*), and *Usnea* sps. were abundant on the trunks and branches of fallen conifers in the clearcuts. Most small mammals ate more invertebrates and fewer conifer seeds in the clearcuts during September than during July. In late summer many insects enter pupal and larval stages within the soil and are more accessible to small mammals (Borror *et al.* 1976). In late summer conifer seeds disseminate and become more abundant on the ground (Fowells 1965). The results of our study indicate that small mammals prefer invertebrates over conifer seeds. Most small mammals ate more invertebrates in burned Clearcut 2 than in the forest and unburned clearcuts.

Salal was the only major vascular plant species, other than conifer seeds, eaten by small mammals in more than small amounts. Salal was abundant in the forest and clearcuts. Grass was not a major component of any small mammal species diet. Native grasses were only occasionally seen in the forest.

The diet of dusky (or montane) shrews (*Sorex monticolus*) was composed of invertebrates, conifer seeds, fungi, and lichens (Table 4). Conifer seeds were an important component in the dusky shrew's diet. The Trowbridge shrew diet was 69-95 percent invertebrates in the forest and clearcuts. These results are similar to those reported by Whitaker and Maser (1976), who found 96 percent insects in Trowbridge shrew stomachs. Shrew mole (*Neurotrichus gibbsii*) diet was 75-88 percent invertebrates during September but mostly conifer seeds (36 percent) and lichens (32 percent) and fewer invertebrates (18 percent) during July.

Fungi and lichens were the major foods eaten by three Townsend's chipmunks (*Eutamias townsendii*) in the forest and burned Clearcut 2 during September (Table 4). Of the eight chipmunk stomachs examined in July, no food preference was found. The "other matter" in their stomachs was pollen. Tevis (1952) also remarked that in conifer forests 99 percent of Townsend's chipmunk stomach content volume is fungi.

The stomach of the one northern flying squirrel caught was entirely of fungal spores. McKeever (1960) found fungi to be the only food of six flying squirrels trapped in summer.

Deer mice ate primarily invertebrates in the forest, conifer seeds in the clearcuts during July, and did not show a preference for any one food in the clearcut during September (Table 4). The stomach of the one deer mouse trapped in the burned Clearcut 2 contained only invertebrates.

TABLE 4. Percent relative frequency of small mammal secies stomach fragments in the forest (F), unburned clearcut trapped in July (CJ), unburned clearcut trapped in Sept. (CS), and unburned clearcut (B). T=Trace.

Food stuff	*Sorex monticolus*			*Sorex trowbridgii*				*Neurotrichus gibbsii*			*Eutamias townsendii*			*Glaucomys sabrinus*	*Peromyseus maniculatus*				*Clethrionomys gapperi*				*Microtus townsendii*		*Zapus trinotaus*
	F	CJ	B	F	CJ	CS	B	CJ	CS	B	F	CJ	B	F	F	CJ	CS	B	F	CJ	CS	B	CS	B	CJ
Fungi, lichen	9	12	1	3	13	1	3	32	15		65	27	68	100	9	22	16		91	55	81	79	100	17	60
Conifer seed pt.	35	26	25	15	9	3	3	36	10			37	18		21	45	27		4	29	15	9			22
Shrub, herb. lf., repro pt.	1	T		1	1	T		2		12	35	5	2		9	1	28			1	2	9		73	10
Grass lf., seed pt.	1	4			1	T									1	3	1		5	4				7	3
Invertebrate pt.	54	51	74	78	69	95	90	18	75	88			12		59	23	27	100		3	2	4			3
Other		6		3	7		4	11				30				5	1			7	T			2	2
Total	100	99	100	100	100	99	100	99	100	100	100	99	100	100	99	99	100	100	100	99	100	101	100	99	100
No. stomachs examined	4	17	4	5	25	30	15	4	1	2	1	8	2	1	7	43	16	1	6	56	45	6	4	2	3

Major food of red-backed voles was lichens in all study plots sampled in July and September (Table 4). The six Townsend voles sampled ate lichens in the clearcut and mostly berries and leaves of bunchberry in burned Clearcut 2. The three jumping mice consumed more fungi (60 percent) and conifer seeds (22 percent), and fewer herbs (10 percent) and grasses (30 percent) than jumping mice collected by Whitaker and Maser (1978) in Mason Co., Washington. They found jumping mice stomach volume as fungi (23 percent), seeds (5 percent), herbs (35 percent) and grasses (34 percent).

Cover, Abundance, and Food Correlations

Dusky and Trowbridge Shrews. Dusky and Trowbridge shrews comprised 8 percent and 24 percent, respectively, of the total catch. Of the total Trowbridge shrews caught in September, 10 percent were in the forest, 60 percent were in Clearcut 3, and 30 percent were in burned Clearcut 2. In contrast, Hooven and Black (1976) found 48 percent of Trowbridge shrew catch in a mature forest, 32 percent in an unburned clearcut, and 20 percent in a burned clearcut. Gashwiler (1970) reported similar results. Both Hooven and Black's and Gashwiler's studies were of longer term (six and ten years, respectively) than ours, and percent ground cover in the clearcuts was lower than in our study. With an 83-90 percent total ground cover in the clearcuts of our study area, we believe shrew microhabitat was improved following logging because shrews were shielded from predators and insects on slash were vulnerable to predation.

Dusky shrews ate more conifer seeds, fungi and lichens, and less invertebrates than did Trowbridge shrews. Both shrews were caught in similar numbers in the forest (Table 3). In Clearcut 1, more dusky shrews were caught than Trowbridge shrews. Dusky shrews, Trowbridge shrews, and deer mice ate fewer invertebrates in this clearcut than those trapped in Clearcut 2 on the same date. The southwest half of Clearcut 2, where our trapping grid was placed, was logged during fall 1979. Timber was not removed until spring 1980. Clearcut 3 was logged with timber removed spring 1980. Insects had a longer opportunity to invade the bark and down wood of southwest Clearcut 2. Insect populations would be expected to be larger in southwest Clearcut 2 than in Clearcut 1. Possibly the Trowbridge shrew population was limited by lack of accessible insects in Clearcut 1.

In the unburned and burned Clearcut 2, and in Clearcut 3, more Trowbridge shrews were caught than dusky shrews. When the largest Trowbridge shrew population was sampled at 30 individuals in Clearcut 3 during September, no dusky shrews were caught. As mentioned earlier, insects are more accessible to shrews in September than in July. We believe that Clearcut 1, which had the largest dusky shrew population, had fewer accessible insects than any other trapped clearcut as a result of logging and trapping dates. Although our study was limited to a specific area and we collected small mammals within a limited time span, we suggest that dusky shrews may be more abundant than Trowbridge shrews in areas of low insect populations because of their ability to alter their diet to utilize other food types. In areas of high insect populations, Trowbridge shrews may outnumber dusky shrews.

Shrew Mole. Shrew moles are burrowing insectivores inhabiting areas of moist soil with dense underbrush and little grass (Dalquest 1948). In our study, as well as in Hooven and Black's (1976) study, few shrew moles were caught. We believe that the immediate

ground cover and soil moisture within the vicinity of a trap, rather than sample plot treatment, was the best indicator of shrew mole presence.

Townsend's Chipmunk. Townsend's chipmunks are the only western chipmunk which live in mature forests. Their numbers increase after forests are logged, and herbaceous and shrubby vegetation becomes abundant (Tevis 1956). We suspect that the lack of Townsend's chipmunks in Clearcut 3 was a result of the large number trapped in the southeast corner of Clearcut 2 (Table 3). Otherwise, our results suggest an increase in chipmunks following logging and burning.

Deer Mouse. Deer mice comprised 22 percent of the catch in the study area. Its populations were largest in unburned clearcuts and lowest in burned Clearcut 2 (Table 3). Ahlgren (1966), Gashwiler (1970), Hooven (1973), Sims and Buckner (1973), and Hooven and Black (1976) reported dramatic increases of deer mice following slash burning. Ahlgren believed that burned clearcuts create habitat and food conditions favorable to increases in populations of seed eating rodents. Williams (1959) found that seeds comprised 66 percent of stomach content of deer mice caught in spruce forests. Deer mice ate more seeds than any other mammal in our study area (Table 4), but the one deer mouse trapped in burned Clearcut 2 ate insects exclusively. Tevis (1956) also found that deer mice ate primarily caterpillars on a recently burned area. We suspect that immediately after a burn, deer mice eat what is available, usually insects. When conifer seeds are planted, or when grassland plant species become established in a clearcut, deer mice alter their diet to consume the most prevalent food, which is then seeds.

Red-backed Vole. Red-backed voles chiefly inhabit the cool, damp forests of western Washington. They burrow under forest litter and nest in hollow logs or under tree roots (Taylor and Shaw 1927, Dalquest 1948). Tevis (1956) considered log cover to be the limiting factor for these voles. Hooven and Black (1976) stated that removal of timber and reduction of vegetative cover on clearcuts reduce the red-backed vole population. Gashwiler (1959 and 1970), Ahlgren (1966), Miller and Getz (1972, 1973, and 1977), and Sims and Buckner (1973) reported a decline in red-backed vole populations following logging. The presence of red-backed voles in clearcuts within the first year after logging spruce forests was noted by Kirkland (1977), Martell and Radvanyi (1977), and West *et al.* (1980). By the third year after logging, Martell and Radvanyi observed that red-backed voles decreased and were rare. With a 65-75 percent overall ground cover from slash and live vegetation in unburned clearcuts, and an abundant food supply of lichens on fallen trees, the red-backed vole population in our study area would be expected to be larger than the population in the forest where there was 55 percent ground cover and fewer accessible lichens. Perhaps when lichens are completely eaten or die in clearcuts, red-backed voles will seek food and shelter elsewhere.

Townsend Vole. Townsend voles are marsh dwellers, often associated with dense grasses and sedges, regardless of elevation. These voles penetrate forest lands wherever the lands are cleared for agricultural purposes (Goertz 1964). Townsend voles are grass and forb feeders (Cook 1959). Grant (1975) stated that *Microtus* have the ability to eat a wide variety of plants which may not occur in grassland habitats. There were few native grasses in our study area, which may explain why Townsend voles ate pri-

marily lichens and bunchberry (Table 4). We believe that Townsend voles are relatively uncommon or rare in the few exposed areas of the forest and then increase in open areas where grasses or lichens are available.

Summary

More small mammals were caught in unburned clearcuts than in the mature forest or burned clearcut. Slash and down material in the unburned clearcuts provided cover and abundant foods—epiphytic lichens, conifer seeds, and insects. Lichens were the principal food eaten by red-backed voles, which were the most abundant small mammal species in clearcuts. Invertebrates were the main food of most small mammals in the forest. No one small mammal species was predominant in the forest.

We caught more dusky shrews than Trowbridge shrews in the clearcut, where we believed the accessible insect population was lowest. We caught more Trowbridge shrews than dusky shrews in the other clearcuts. Only one deer mouse was caught in the burned clearcut, compared to 17 caught in the unburned clearcut trapped on the same dates. This single deer mouse's stomach content was entirely invertebrates. In the forest and unburned clearcuts deer mice did not consume any one particular food type. Townsend's voles and jumping mice were found in low numbers in clearcuts. Both species ate more fungi and lichen and fewer grasses than past studies have indicated. Grasses were uncommon in the study area.

Small mammals ate a higher percentage of invertebrates in clearcuts trapped in September than in July. As invertebrate consumption increased, fewer conifer seeds were eaten. Insects are more accessible to small mammals in September, and conifer seeds are more abundant in late summer. We suggest that small mammals, especially Trowbridge shrews, shrew moles, and deer mice, prefer insects over conifer seeds if both food types are abundant.

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Dispersal of a Yearling Male Black-tailed Deer

Abstract

A male black-tailed deer (*Odocoileus hemionus columbianus*) inhabited a home range of 11.1 ha during May and June while 10 to 11 months old. In late June, near its first birthday, it dispersed 16.8 km in 8 days to occupy a new home range of 8.7 ha in similar habitat. Its movements were non-random and highly directional (Rayleigh test, $P < 0.05$).

Introduction

Dispersal is defined by Howard (1960) as the movement an animal makes from its point of origin to the place where it reproduces or would have reproduced had it survived and found a mate. Caughley (1977) noted both the importance of dispersal to population processes and the difficulties associated with documenting disperal. The short duration of dispersive movements makes detailed observations fortuitous. Although there are many studies of deer movements (Zwickle *et al.* 1953, Carlsen and Farmes 1957, Brown 1961, Zalunardo 1965, Robinette 1966, Alexander 1968, Hawkins *et al.* 1971, Harestad 1979) few report the movements of individuals during dispersal (Sparrowe and Springer 1970). Documented accounts of dispersal are equally rare for other mammals (Shirer and Downhower 1968, Storm *et al.* 1976). Herein we report observations of post-juvenile dispersal by a yearling, male black-tailed deer (*Odocoileus hemionus columbianus*).

Study Area and Methods

Observations were made in the Nimpkish River drainage of Vancouver Island, B.C. (15°13′N, 126°36′). The area is mountainous, with valley bottoms at 160-400 m in elevation and many peaks reaching over 1500 m. Biogeoclimatic zones represented in the study area are the Coastal Western Hemlock Zone at lower elevations (200-900 m), the Subalpine-Mountain Hemlock Zone at upper elevations (800-1500 m), and the Alpine Zone near mountain tops (above 1500 m) (Krajina 1965). Forest harvesting began in the study area about 1945. Logging has resulted in a forest ecosystem containing a mixture of recently cut trees (cutovers), second-growth stands, and old-growth stands. Nineteen black-tailed deer were immobilized and fitted with radio-collars during the study (see Harestad (1979) for details regarding equipment and

drugs). Most deer were adult, and detailed observations on dispersal were obtained for only a single individual. On 4 May 1975 a male (OFL59), less than one year old, was immobilized and fitted with a radio collar. Because births in the study area are concentrated between 1 June and 1 July, its age was estimated as between 10 and 11 months. Its movements were followed from 4 May to 17 September 1975. Three to five bearings were used to estimate transmitter locations. Some locations were visual. Home range was calculated using the minimum home range method (Dalke and Sime 1938).

Results and Discussion

During the period 5 May through 21 June 1975 the home range of OFL59 extended over 11.1 ha ($n=23$). This area is within the range of home range sizes exhibited by non-parturient, adult black-tailed deer within the study area (Harestad 1979). The home range centered in a patch of small conifers and had a standard distance deviation of 178 m. Habitat consisted of three recently logged areas ranging in age between 1 and 12 years, and a stand of old-growth timber.

The open cutovers were used primarily during the night and crepuscular periods, whereas the old-growth timber was used during the day. A residual strip, 18 m wide, between two cutovers was frequently used as bedding habitat during the day. This residual strip contained unburned debris and small residual conifers remaining from logging operations, most between 1-4 m high.

Farther south on Vancouver Island at Northwest Bay (49° 13′N, 124° 18′W), only one of 18 deer (5.6 percent) moved out of its natal area during its first year of life (Bunnell and Harestad, unpubl.). The home range documented for OFL59 during the period 5 May through 21 June probably was its natal home range. Documented home ranges of black-tailed deer in the study area were no greater than 2.3 km in diameter, and migratory movements did not exceed 5 km (Harestad 1979). On 24 June, OFL59 was sighted crossing a road 9.5 km southwest of his former home range. Locations were made daily during the next week. His route crossed the Davie River, the Nimpkish River, and then halted briefly near the north end of Woss Lake (Fig. 1).

At 0820 on 25 June, he was located 12.4 km from his former (likely natal) home range in a 15-year-old conifer plantation near Woss Lake. Later that day (1200 hrs) he was sighted walking along the road 0.9 km south along the eastern shore of the lake. At 1310 on 26 June, he was back near his early morning location of 25 June and in a small patch of old-growth forest surrounded by conifer plantations.

The signal could not be heard near Woss Lake on 28 June, but was located 3.9 km further west in the Eve Creek drainage on 29 June. He remained in this area until 5 September. The new home range covered 8.7 ha and had a standard distance deviation of 246 m. The smaller size of the new home range may be the result of fewer locations ($n=8$). The new home range centered on a patch of conifer residuals and advanced regeneration located along a ridge in a 7-year-old cutover and in habitat similar to his previous home range.

The route followed by OFL59 was directional; using the Rayleigh test (Durand and Greenwood 1958), it is highly unlikely to be a result of random movement ($\underline{z}=3.32$, $n=8$, $\underline{P}\leq 0.05$). He moved from his initial home range and occupied his

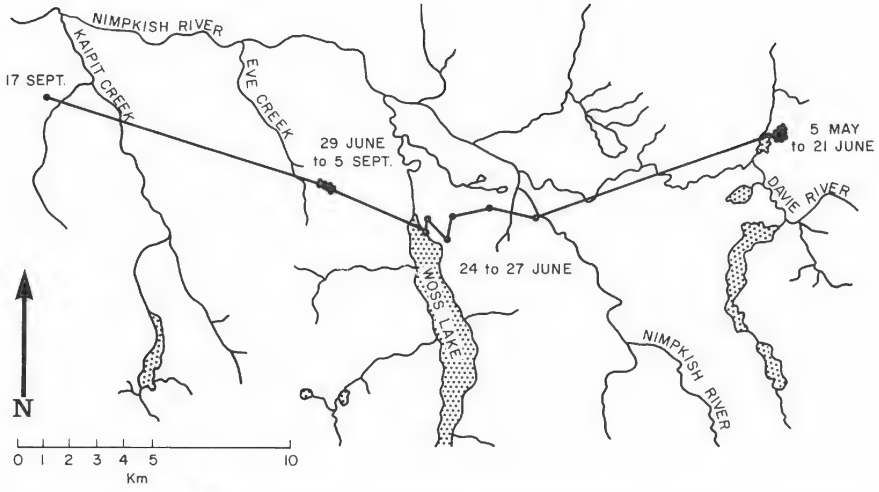

Figure 1. Locations (●) of a dispersing, juvenile black-tailed deer from 5 May to 17 September 1975.

new home range in 8 days, at most. The two home ranges were 16.8 km apart in straight line distance.

After occupying his new home range from 29 June to 5 September, OFL59 moved 11 km westward (Fig. 1). This movement coincided with the opening of hunting season. The new area was remote, and only approximate locations could be obtained. OFL59 was found dead the following year. The marrow in the femur was white and solid, and the antlers were still attached to the skull, suggesting that he died before the end of December 1975. The remains were not scattered and the ribs intact, suggesting death was not from predation. The disappearance of OFL59 from his new home range at the commencement of hunting season and the condition of his remains suggest that OFL59 was wounded, moved from his new home range, and subsequently died. This final movement was probably atypical of a dispersing juvenile deer.

There are few comparable observations of black-tailed deer against which the generality of our findings can be evaluated. Dispersal occurred near the animal's first birthday, was short-lived, and was directional over a distance of 16.8 km. At Northwest Bay, analyses of returns from 62 of 266 marked fawns indicated that disperal occurred most frequently when deer were 1-2 years old, that dispersal was directional, and that dispersive movements averaged 15.2 km (Bunnell and Harestad, unpubl.). Brown (1961) reported that black-tailed deer in Washington also dispersed most often when 1-2 years old; dispersive movements averaged 9.5 km (our computations from data of Brown (1961: Tables 15 and 16). Hedlund (1975) reported four dispersive movements by *O. h. hemionus* in Washington. All were male. Three of the four were killed as yearlings, the fourth when 2.5 years old. Average distance dispersed was 66 km (Hedlund arbitrarily assumed 16 km as the distance distinguishing local movement from dispersal). Neither Brown (1961) nor Hedlund (1975) provided individual movements so it is unclear whether dispersal was directional. Sparrowe and Springer (1970; Fig. 4) reported movements of a yearling male white-tailed deer (*O. virginianus*),

but indicated that it was harassed by hunters. The deer moved 4 km prior to hunting season and then traveled about 36 km before settling in a new area, where it was shot. There was no apparent directionality to its movements. Kammermeyer and Marchington (1970) provided distances for three breeding-age male *O. virginianus*, but not individual movements. Mean distance dispersed was 4.5 km.

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Rhythmic Locomotor Activity in the Intertidal Shorecrab Hemigrapsus oregonensis (Brachyura, Grapsidae) from the Oregon Coast

Abstract

Sixteen adult male shorecrabs, *Hemigrapsus oregonensis* (Dana 1851), were collected from the 1.52 m (+ 5 ft) level at Coquille Point in the Yaquina Bay Estuary (44° 37′ N. Lat., 124° 04′ W. Long.), Oregon, U.S.A. The crabs were held in testing chambers at 10° ± 1° C under varying artificial light conditions. About half of the crabs showed both a tidal and a diurnal rhythmicity. The activity progression reflected greatest activity during predicted periods of dark-high tide at the collection site followed by dark-low tide followed by light-high tide, with least activity occurring during periods of light-low tide. Results are based on over 3000 h of monitoring time.

Introduction

Hemigrapsus oregonensis is a common inhabitant of the North American intertidal from Alaska to the Gulf of California (Schmitt 1921, Hart 1968). Within this range, it is most common in habitats ranging from muddy to a pea-sized gravel substratum (Way 1917, MacKay 1943, Hiatt 1948, Ricketts *et al.* 1968). It is quite tolerant of high silt loads and is considered to be both euryhaline and eurythermal (Dehnel 1960, Gross 1963, Dehnel and Carefoot 1965).

The periodicity of the tides, as expressed in varying exposure times at different tidal levels, would be expected to exert a great influence on the foraging patterns and behavioral activities of intertidal organisms. Tidally linked behavioral rhythms have been demonstrated in numerous marine organisms, including clams (Bennett 1954), oysters (Loosanoff and Nomejko 1951), prawns (Rodriquez and Naylor 1972), amphipods (Fincham 1970), isopods (Enright 1971, 1972), and several species of intertidal crabs (Fingerman 1955, Naylor 1958, Williams 1966). *H. oregonensis*, which is exposed to a fluctuating tidal regime, might be predicted, then, to exhibit tidally linked behavioral rhythms. The present study attempted to determine if locomotor activity patterns existed and, if so, to determine if they were related to a fluctuating tidal regime.

Methods

Adult male crabs with a minimum carapace width of 2.5 cm were collected during October and November 1972, during low tide at Coquille Point in the Yaquina Bay Estuary (44° 37′ N. Lat., 124° 04′ W. Long.) on the central Oregon coast from the 1.52 m (5 ft) tidal level. They were immediately transported to the laboratory in Corvallis, Oregon, about 80 km (50 mi) inland. Experiments were initiated within 3 h

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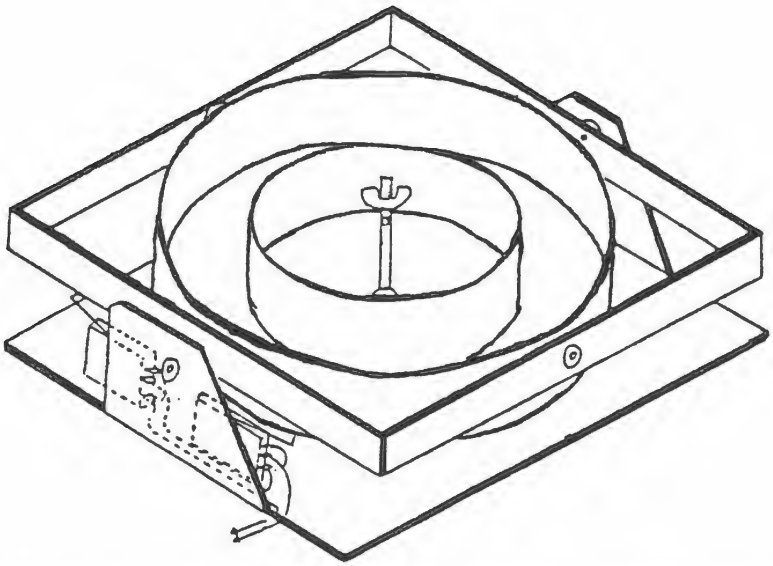

Figure 1. Activity chamber used in locomotor analysis of *Hemigrapsus oregonensis*. Chamber was suspended from yoke and gimbal framework to allow displacement in any plane from the horizontal. Microswitches were activated when the crab crossed an axis of rotation. Microswitches were connected to an Esterline-Angus event recorder which allowed continuous activity monitoring. Activity events were recorded as vertical marks on the continuously moving chart and were tabulated as number of events per hour.

after removal from the collection site and before the next high tide would have covered the collection area. All activity experiments were conducted in a cold room maintained at 10° ± 1° C. The crabs were placed in an activity chamber, one per chamber, and their locomotor activity responses monitored for up to nine consecutive days. The animals were not fed during the experimental period. The test chambers (Fig. 1) were constructed from two cyclindrical pieces of plexiglass 5 cm high, one having a diameter of 15 cm and the other a diameter of 25 cm. The smaller diameter piece was placed into the larger piece and spaced evenly to give a circular runway. The floor of the chamber was fitted with sea water saturated filter paper, and a lid was placed over the chamber to prevent the crab from escaping. The chamber was suspended from a ballbearing pivoted yoke and gimbal framework. Because the pivotal axes were at right angles to each other, the suspended activity chamber could be tilted in any direction. Microswitches were placed under the movable frameworks. Each time a crab crossed a quadrant of the chamber (rotational axis), the displacement of the chamber activiated a microswitch mechanism. The microswitches were connected to an Esterline-Angus 12 volt D.C. series 80 M continuous event recorder. The number of activity events per hour were counted and compared with the natural daylight (sunrise-sunset) hours and the tidal regime during the experimental period. The light regime in the experimental chamber (abrupt lights on-lights off) was, early in the experiments, identical in length to the natural sunrise-sunset period but was later reduced to a constant low level red light (dark) regime. The tidal regime during the study period was established by plotting

the predicted mixed semi-diurnal tidal heights and then calculating the time during which the 1.52 m (5 ft) tidal height (from which the crabs were collected) was covered and exposed both during natural daylight and night time periods. No distinction was made between the collection site being covered by a lower high tide or a higher high tide. The length of time the collection site was covered by either type of high tide was, however, a major consideration. The number of activity events per hour was compared between periods of light, dark, covered (high tide) exposed (low tide), and several combinations of these. Student's t-test between means was applied as a statistical test to determine if significant variation in activity patterns correlated with natural light or tidal cycles. Results are based on over 3000 h of total monitoring time, an average of 190 h monitoring time on each of 16 individual male crabs.

Results

Subjective field observations suggested greater crab activity during night low tide periods than during day low tide periods. Experiments were performed to determine if this apparent day-night difference existed. Additional experiments were performed to determine if activity periods were regulated by a solar day cycle (light regime), a lunar day cycle (tidal regime), or a combination of both. Data showed that subjective field observations were not valid in all cases. In about half of the experiments, less activity occurred during dark periods than during light periods. Activity seemed most dependent on the state of the tide, however. Greatest activity occurred during high tide periods, regardless of the light regime. Both solar day (24.0 h) and lunar day (24.8 h) length seemed to affect crab activity patterns.

The activity pattern of one crab over a five day period under a natural light regime (L = 12 h, D = 12 h) (Fig. 2) has been superimposed on the tidal regime during the experimental period. This crab had activity bursts coinciding with periods of high tide. Both low tide and dark periods were periods of low activity. Few crabs were ever seen moving about during daytime low tide at the collection site, suggesting that periods when the crabs were covered (high tide) were periods of increased activity. The mean length between activity bursts was found to be 24.6 h, corresponding quite closely to a 24.8 h periodicity between successive higher high tides.

Figure 3 shows a persistent activity rhythm over seven tidal cycles. However, rather than relatively low activity during darkness, great activity bursts were recorded during periods of light or high tide. The mean length between bursts was 12.2 h, almost half that of the lunar periodicity. The periods of greatest activity were not precisely coincident with periods of high tide. The crab's activity peaks preceeded the predicted high tide by about 3 h. Not all crabs showed a clear rhythmic pattern when subjected to a light-dark regime. Some crabs showed decreasing activity during the experiment. In one case, an average of 9.7 events per hour was recorded for the first two tidal cycles, but by the sixth and seventh tidal cycles only 2.3 events per hour were recorded. The greatest hourly activity in this less active crab corresponded to the initiation of dark and light periods.

It was apparent, then, that not all crabs exhibited a well-defined locomotor activity rhythmicity. Since it was indicated that both light and high tide may be cues for initiating activity periods, an experiment was run to minimize the effects of light on the apparent activation of the crabs. Two additional crabs were subjected to a natural (L = 7 h, D =

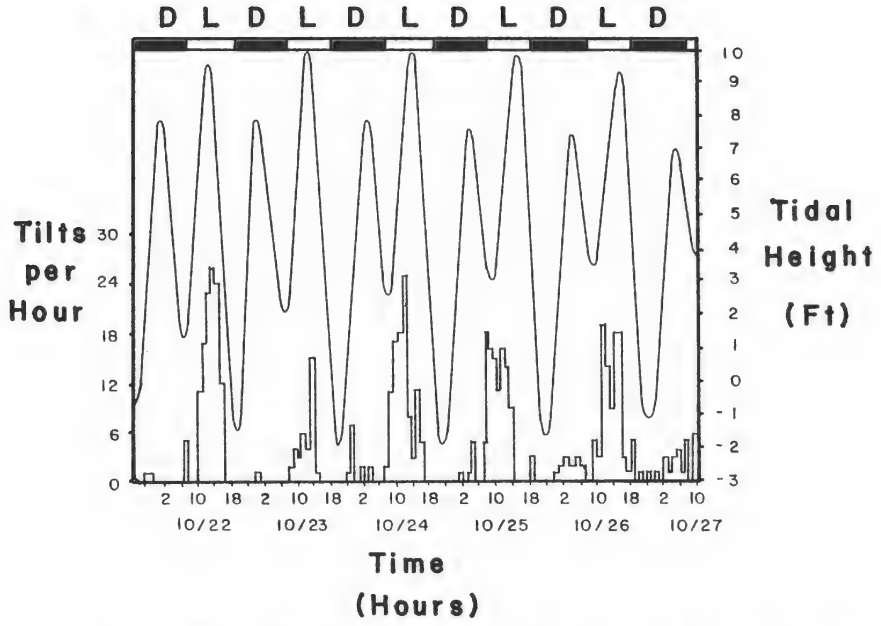

Figure 2. Activity pattern of an isolated *Hemigrapsus oregonensis* subjected to an artificial light regime (L = 12h, D = 12h). The activity pattern is superimposed on the predicted tidal regime at Coquille Point in the Yaquina Bay Estuary, Oregon.

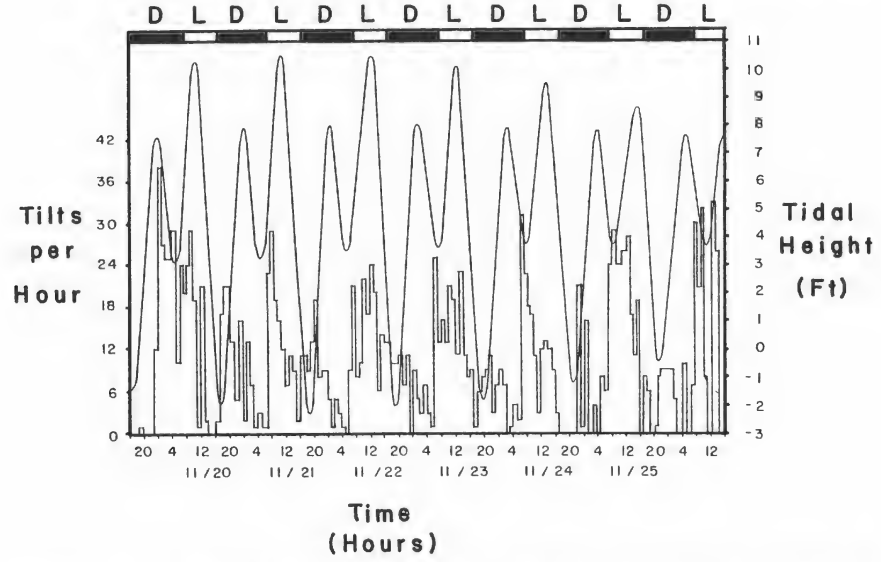

Figure 3. Activity pattern of an isolated *Hemigrapsus oregonensis* subjected to an artificial light regime (L = 7h, D = 17h). The activity pattern is superimposed on the predicted tidal regime at Coquille Point in the Yaquina Bay Estuary, Oregon.

17 h) light-dark regime for three full tidal cycles and then denied any light intensity increases for the next six full tidal cycles. A clear rhythmicity emerged after the crabs were subjected to constant darkness. Since the light regime was not in effect, the rhythmicity which emerged (Fig. 4) presumably was not cued on increasing light intensity (solar regime). The mean length between activity bursts was 29.0 h, with an average duration of 21.6 h. It thus appeared that under constant darkness the periodicity of the locomotor response tended to expand and become out of phase with the high tide within five tidal cycles.

Similarly, Figure 5 shows a definite rhythmicity emerging during the constant dark

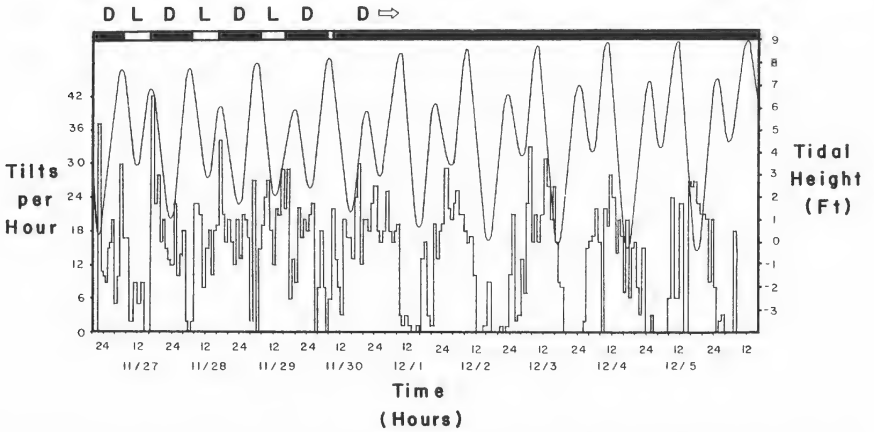

Figure 4. Activity pattern of an isolated *Hemigrapsus oregonensis* subjected to an artificial light regime (L = 7h, D = 17h) for the first three photoperiods and then subjected to a constant low level light regime for the next six consecutive tidal cycles. The activity pattern is superimposed on the predicted tidal regime at Coquille Point in the Yaquina Bay Estuary, Oregon.

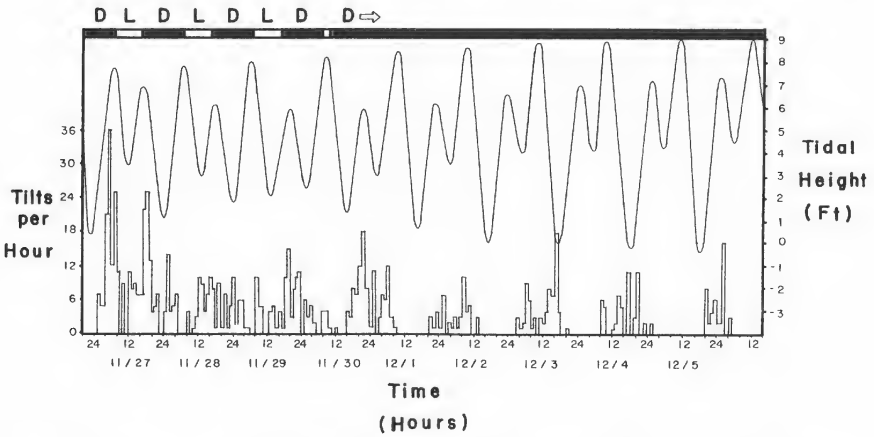

Figure 5. Activity pattern of an isolated *Hemigrapsus oregonensis* subjected to an artificial light regime (L = 7h, D = 17h) for the first three photoperiods and then subjected to a constant low level light regime for the next six consecutive tidal cycles. The activity pattern is superimposed on the predicted tidal regime at Coquille Point in the Yaquina Bay Estuary, Oregon.

portion of the experiment. The average duration between activity bursts was again 29.0 h, suggesting an endogenous rhythmicity which was longer than the lunar day cycle (24.8 h). Additional experiments under constant darkness showed initial activity peaks corresponding to high tide periods during the first two or three tidal cycles, but later appearing to become more random. The interval between activity peaks before disintegration of the pattern was considerably less (25.7 h and 23.0 h) than the 29.0 h periodicity found in those activity patterns which did not decay.

It was suspected, then, that two different entrainment factors were operative: light regime and tidal regime. The periodicity of activity relative to light, dark, and to whether the habitat was covered (high tide) or exposed (low tide) was investigated. A t-test between mean number of events per hour indicated that the crabs that exhibited a rhythmic cycle were significantly more active ($p < .05$) during periods of darkness than during periods of light. These crabs were also more active ($p < .05$) during periods of high tide than during periods of low tide, during periods of high tide than during light ($p < .05$), and during darkness than during low tide ($p < .05$). It thus appeared that greatest periods of overall activity occurred during high tide; the next greatest period of activity coincided with darkness followed by low tide, and with least activity recorded during daylight hours.

Periods of darkness were further divided into dark-high tide and dark-low tide periods. Light periods were similarly divided into light-high tide and light-low tide periods in an effort to couple the light regime and tidal regime effects. Greater crab activity ($p < .05$) occurred during light-high tide than during light-low tide, reflecting a true tidal rhythmicity. Greater activity ($p < .05$) occurred during dark-high tide than during light-high tide, suggesting a diurnal rhythmicity. Greater activity was also found during dark-high tide than during light-low tide. In order of decreasing magnitude, the greatest activity was found during dark-high tide followed by dark-low tide followed by light-high tide, with least activity recorded during light-low tide periods.

In some crabs, however, a comparison of activity during the light regime with the combined effect of the tidal regime indicated that the greatest activity occurred during periods of light-low tide followed by light-high tide, with equal activity during dark-high tide and dark-low tide (means not significantly different at .05). These findings support the interpretation that for some crabs the rhythmicity due to tidal fluctuation is absent or completely masked by the light regime rhythmicity.

The results of t-tests between mean number of events per hour showed that, in the absence of reinforcing light or tidal stimuli, greater activity occurred during predicted dark periods than during predicted light periods or predicted low tide periods ($p < .05$). Activity was also greater during high tide than during low tide ($p < .05$) or during daylight ($p < .05$). During dark periods, greater activity occurred during high tide than during low tide ($p < .05$). During light periods, however, no statistical differences ($p > .05$) were found between means at high tide and low tide. During high tides, greater activity occurred during dark hours than during light hours ($p < .05$). Similarly, during low tides greater activity was found during darkness than during light hours ($p < .05$). Under a constant dark regime, then, some crabs were still capable of maintaining a rhythmicity based on both tidal cycles and light cycles; others, however, under the same conditions apparently lost the tidal component. In those crabs that showed both a diurnal and a tidal rhythmicity under constant darkness, the activity

progression was the same as for those under the experimental light regime: greatest activity during predicted dark-high tide followed by dark-low tide followed by light-high tide with least activity during light-low tide.

Discussion and Conclusion

Symons (1964) found variability in locomotor activity (walking behavior) of *Hemigrapsus oregonensis*. Although he did not investigate tidally linked rhythms, he did demonstrate a diurnal component in male crabs, with maximal activity occurring during dark hours (0530 h, ½ ft-c). During this study, periods of activity in *Hemigrapsus oregonensis* were also found to be quite variable. Not all crabs tested showed a rhythmicity of locomotor patterns. Similarly, only about 50 percent of tested fiddler crabs (*Uca crenulata*) showed a rhythmicity (Honegger 1973). *Hemigrapsus edwardsi* from New Zealand showed a seasonal variation in activity which corresponded to vertical migrations in the intertidal (Williams 1969). During warmer water months (December, January, February) *H. edwardsi* showed a persistent tidal rhythm, with peak activity occurring one or two hours preceeding high tide. This tidal rhythm, however, was not as apparent during cold water months (June, July, August), when the crabs would migrated down into the lower regions of the intertidal. Under constant conditions, this crab would lose its tidal periodicity after two to three weeks; but, under the same constant conditions, it would slowly re-establish its rhythmicity. The cue for initiating this re-entrainment was not established, but it was thought to be endogenous in origin.

H. edwardsi seems to lack a strong circadian component. The crabs *Sesarma reticulatum* and *Carcinus maenas* displayed a tidal and a diurnal rhythm for about three to four days, with peak activity bursts at a periodicity of 24 h (diurnal component) and 12.4 h (tidal component). Maximum activity during the tidal component occurred during high tide periods.

About half of the *H. oregonensis* were shown to display tidal and diurnal rhythmicities. Greatest activity occurred when the collection site was covered by high tide and was usually intensified during dark hours.

It is speculated that *H. oregonensis* is most active at high tide periods when moving from cover would not result in excessive dessication, heating, or predation from shorebirds. Activity also appears to be greatest when high tide was coupled with darkness. During these conditions (dark-high tide), it is speculated that foraging would present the least chance for visual detection by fish predators.

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Trace Element Content of Leaves of Desert Shrubs in South-central Washington

Abstract

Analyses of leaves of desert shrubs showed strong differences in macroelements according to species and location on the Arid Lands Ecology (ALE) site in south-central Washington. Halophytes were characterized by high levels of K, Cl, Br, Mn, and Na, and glycophytes by high levels of Ca and Mg. However, trace element content was not significantly different. Big sagebrush (*Artemisia tridentata*) leaves from Wyoming and the ALE site were not greatly different in trace element content. Natural leaf fall collections can be used to monitor changing levels of trace element content induced by coal combustion steam-electric plants.

Introduction

Measurements of the mineral content of leaves of desert shrubs growing in the shrub steppe region of south-central Washington have generally centered upon mineral cycling behavior (Mack 1977, Rickard 1965, Rickard and Keough 1968, Cline and Rickard 1974) and have been mostly concerned with the behavior of macronutrient elements and sodium rather than trace metals. In recent years considerable attention has been paid to trace metals as soil-plant contaminants because some of these are potentially toxic, and also because trace metals are released into the air in large quantities at large coal combustion steam electric plants even after pollutant suppression devices are installed (Vaughan *et al.* 1975, Turner and Strojan 1978). After many years of coal burning, trace metals can be expected to show elevated levels in soils near coal-fired plants. With elevated levels of trace metals on and mixed in the rooting substrate, elevated levels may eventually occur in the leaves of plants as the metals are moved into the root zone by leaching, freezing, thawing, and other processes.

Connor *et al.* (1976) measured trace metals in soil and big sagebrush (*Artemisia tridentata*) leaves at various distances from an operating coal-fired power plant in the Powder River Basin region of northeastern Wyoming and showed elevated levels of strontium, vanadium, and selenium in leaves; these levels were attributed to smoke stack emissions. Like many parts of the semi-arid western United States, big sagebrush is the most abundant shrub on the ALE site in Benton County, Washington.

This investigation determined the trace element content of freshly fallen leaves of four desert shrub species on the ALE site and indicates that freshly fallen leaves can be employed to monitor levels of trace metals that might result from future operation of coal-fired steam-electric power stations in the semi-arid shrubsteppe region of south-central Washington and adjacent Oregon. Historically, southeastern Washington

has been relatively free from coal burning because the electrical requirements of the region have been mostly provided by hydroelectric dams and nuclear power.

Methods

Newly fallen leaves were collected in 1978 from four desert shrub species by placing non-metallic containers beneath the canopy spread of four individual plants of each species and by collecting the newly fallen leaves at monthly intervals (Rickard and Warren 1981). The leaf collections at the peak litterfall month, 2 g or more, were air dried, pooled, and homogenized by grinding to a fine powder with a Wiley Mill. Aliquots of each sample were dissolved by refluxing in a nitric/perchloric acid mixture (4:1). Analysis utilized several techniques. Argon inductive coupled plasma spectroscopy was used to analyze simultaneously for Ca, Mg, Na, K, P, Al, Ba, B, Cu, Fe, Mn, Sr, and Zn. Chromium, Co, Mo, Ni, V, Pb, and Sb were analyzed using graphite furnace atomic absorption spectroscopy. Bromium and Cl were determined by neutron activation and subsequent gamma spectroscopy. Arsenic and Se were determined by atomic absorption spectroscopy of the separated hydrides. All tissue samples were analyzed in duplicate and run concurrently with National Bureau of Standards reference biological standards.

Results and Discussion

The mineral content of newly fallen leaves of *Artemisia tridentata, Purshia tridentata, Atriplex spinosa,* and *Sarcobatus vermiculatus* is summarized in Table 1. These species

TABLE 1. Mineral content of freshly fallen leaves of desert shrubs analyzed on the month of peak leaf fall in 1978. Results are ppm dry weight.

	GLYCOPHYTES			HALOPHYTES	
	Artr	Artr	Putr	Atsp	Save
Ca	16,700	17,500	11,600	9,100	11,600
K	12,200	10,800	10,700	27,500	9,610
PO_4^3	6,820	3,680	1,970	5,500	2,420
Mg	2,450	1,460	7,100	7,850	1,490
Cl	1,510	1,770	4,630	9,500	14,400
Fe	1,420	1,250	1,300	1,200	695
Al	990	950	860	850	505
SiO_2	300	290	450	390	350
Na	250	140	170	1,190	95,000
Mn	180 (30-100)[1]	90	93	147	202
Ti	120 (70-300)	140	121	90	75
B	73 (20-30)	74	77	40	59
Sr	61 (30-200)	45	54	27	38
Ba	34 (50-150)	17	28	18	13
Zn	27 (27-55)	14	14	14	4.1
Cu	15 (15-20)	11	10	5.9	8.3
Br	15	9	46	120	555
Pb	5.0 (5-20)	8.9	12	3.1	3.9
Mo	2.3 (0.7-1.5)	2.0	2.4	6.0	1.9
V	2.0 (3-10)	2.0	2.5	2.0	1.0
Ni	1.2 (1-3)	1.4	2.2	2.0	1.4
Cr	1.1 (1.5-7)	.90	12	1.6	.70
As	.91	.42	8.3	1.4	.20
Co	.40 (0.2-0.6)	.30	.30	.30	.40
Sb	.12	.13	.95	.08	<.05
Se	.11 (0.2-1.6)	<.05	.10	.58	.55

[1]Range of values determined for big sagebrush (**Artemisia tridentata**) leaves collected in Wyoming. Data are from Connor **et al.** (1976). Data have been adjusted assuming an ash weight of 10 percent of dry weight for sagebrush leaves.

represent three plant families: Compositae (*Artemisia*), Rosaceae (*Purshia*), and Chenopodiaceae (*Sarcobatus* and *Atriplex*) and two ecological categories, glycophytes and halophytes. The halophytes were generally characterized by high levels of potassium, chloride, bromide, manganese, and sodium. *Artemisia* was characterized by relatively high levels of calcium, and *Purshia* and *Atriplex* had relatively high levels of magnesium. *Sarcobatus* was low in iron and aluminum. The trace metal content of shrub leaves was not greatly different, regardless of species or location; however, zinc was low in *Sarcobatus*, and arsenic and chromium were relatively high in *Purshia.*

To detect temporal changes in trace metal content of rangeland plants, it is desirable to sample the same individuals (non-destructive sampling) at the same time of year over many years. This procedure can reduce the inherent trace element variability associated with sampling of different plant tissues at different locations and different times of the year; it also avoids the mixing of leaves of different physiological ages.

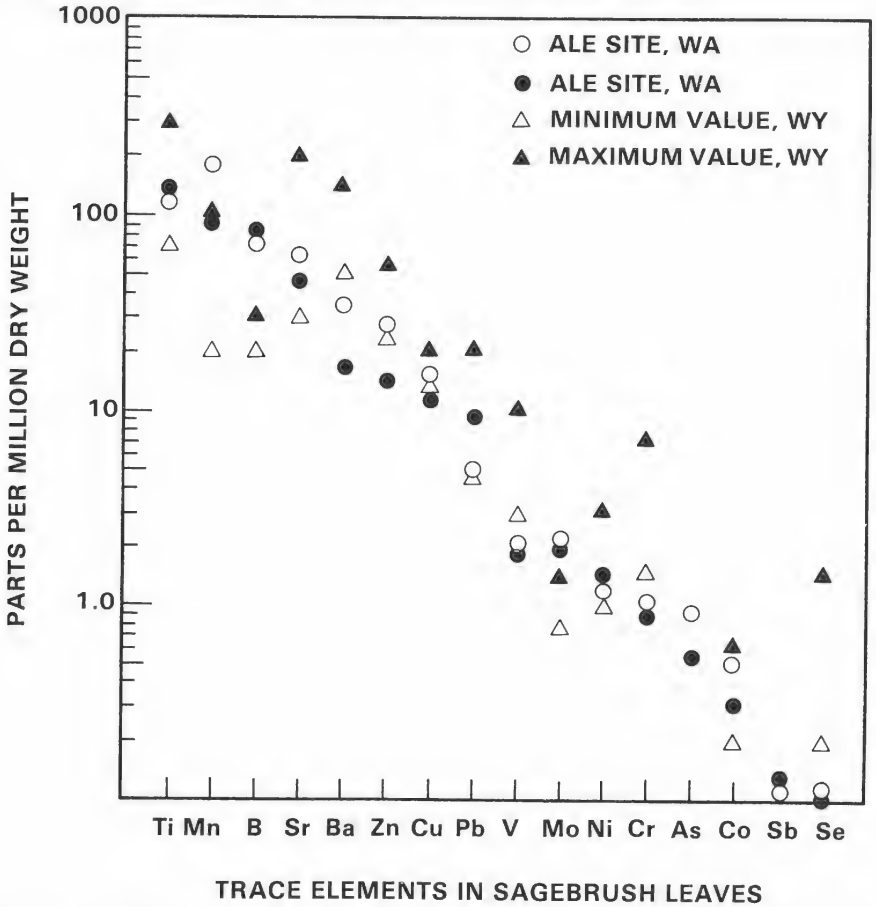

Figure 1. Trace element content of big sagebrush (*Artemisia tridentata*) leaves collected from two sites on the ALE Site, Washington, compared with minimum and maximum values from Wyoming.

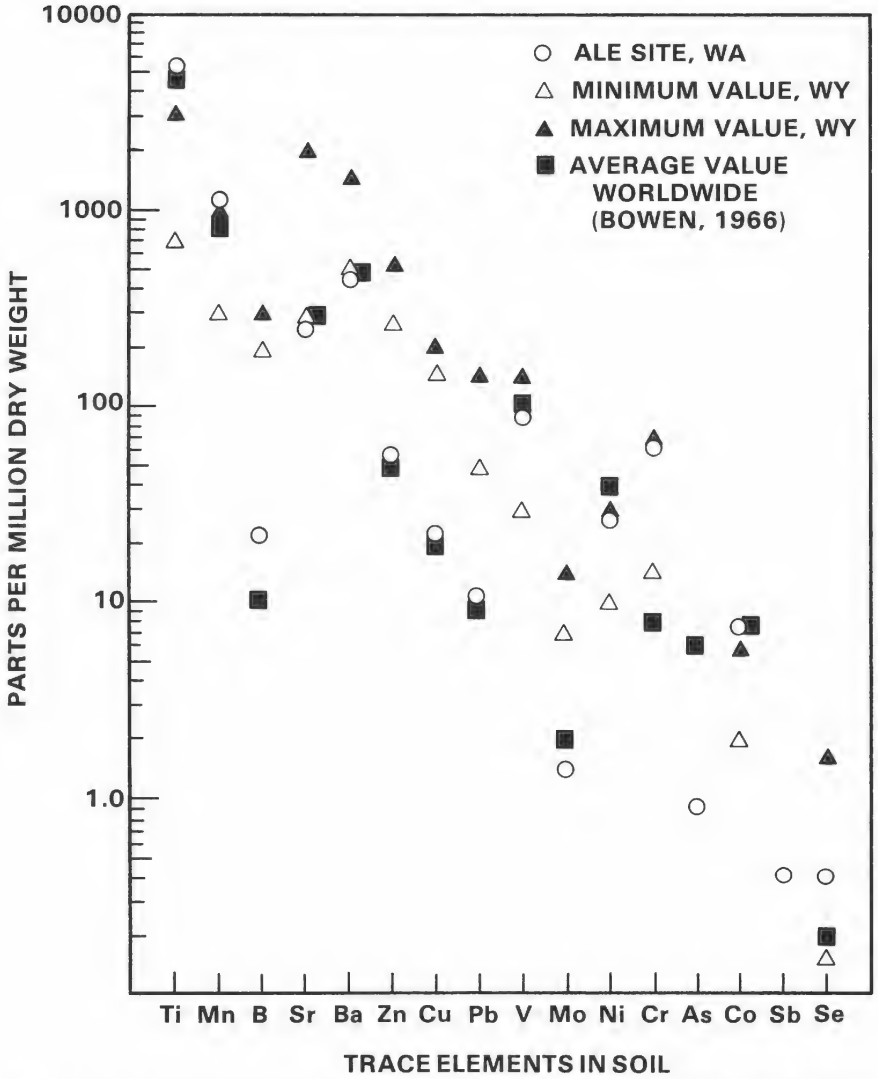

Figure 2. Trace element content of soil from the ALE Site, Washington, compared with minimum and maximum values from Wyoming.

Desert shrubs are long-lived plants, and individual mature shrubs can be expected to be available for sampling for several decades. However, desert shrubs are occasionally exposed to destruction by fire, and new sampling locations may need to be selected from time to time as losses to wildfire occur. Litterfall collectors placed beneath the shrub canopy of individual plants provides a repeatable non-destructive way to sample senescent leaves through normal leaf fall. The trace metal content of these leaves represents external (surface) retention as particulates as well as trace metals delivered internally

to leaves via the soil-root-shoot pathway. Big sagebrush leaves collected from Washington and Wyoming indicate that trace metal content is not markedly different (Table 1).

Graphic presentations of trace element content of big sagebrush leaves and soil samples from Washington and Wyoming are shown in Figs. 1 and 2. When arranged in decreasing order of abundance, titanium and manganese are most abundant in sagebrush leaves and soil. Cobalt, antimony, and selenium were least abundant. In general, the same order of trace element abundance is displayed between sagebrush leaves and soil. Some of the measured trace element content in leaves probably represents surface contamination by dust. To establish whether elevated soil concentrations of trace metals can induce elevated levels of trace elements to sagebrush leaves via root uptake processes will require novel experimental procedures and designs to distinguish surface contamination from root uptake contamination (Straughan *et al.* 1981). Because big sagebrush is much more abundant in the study area than other shrub species, it seems likely that it offers the best opportunities for long term monitoring.

Acknowledgment

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Geophysical Investigation of Southeastern Puget Sound, Washington

Abstract

The presence of a recently active fault, striking northwest through the Lower Puyallup Valley and Commencement Bay adjacent to Tacoma, Washington, may explain the conspicuous agreement among various types of geophysical and geological data. The data, including geomorphology, macroseismicity, temporal elevation changes, and gravity, exhibit a linear feature with an apparent vertical velocity on the order of 8mm/year. Evidence of past geothermal activity may also be associated with this lineal feature.

Introduction

The Puget lowland is an elongated, slightly convex eastward, crustal depression extending from the Strait of Georgia, British Columbia, to Olympia, Washington. Research within the lowland for almost a century has indicated that the area has been tectonically active (Willis 1886, 1889; Bowie 1924; Mullineaux *et al.* 1959; Neumann 1959, 1961; Danes *et al.* 1965; Crosson 1972-1978; Wilson *et al.* 1979; Yount and Gower 1981). Faults associated with this activity have only recently been recognized (Neumann 1959, Danes *et al.* 1965, Rogers 1970, Couch 1970, Gower 1978, Wagner *et al.* 1980, Yount and Gower 1981). In particular, R. W. Couch (unpub. ms.) presented temporal elevation changes in the Puget lowland region (Fig. 1). In summary, Couch found large zones of relative uplift in the Bellingham and Olympia areas, and zones of relative subsidence east of Everett and near Auburn (south of Seattle and east of Tacoma). A striking result of his study is a lineal transition zone between the Auburn depression and the Olympia uplift. The transition zone trends about N. 45° W. through the Puyallup Valley and has an apparent vertical velocity on the order of 8mm/year.

The intent of this paper is to clarify the nature of this lineal, temporal elevation transition zone by presenting more specific geological and geophysical data from the area directly influenced by this anomaly.

Geologic Setting

Consolidated Deposits

Sedimentary and volcanic bedrock is exposed along the southeastern and northern boundaries (Fig. 2) of the study area. These Eocene sediments (Mullineaux 1965, Gard 1968) consist of marine to freshwater sandstone, siltstone, shale, and coal, with locally interstratified volcanic sedimentary rocks. The total thickness is reported to be in excess of 3.3 km (Gard 1968).

Irregularly shaped bodies of porphyritic andesite (Mullineaux 1965) have intruded

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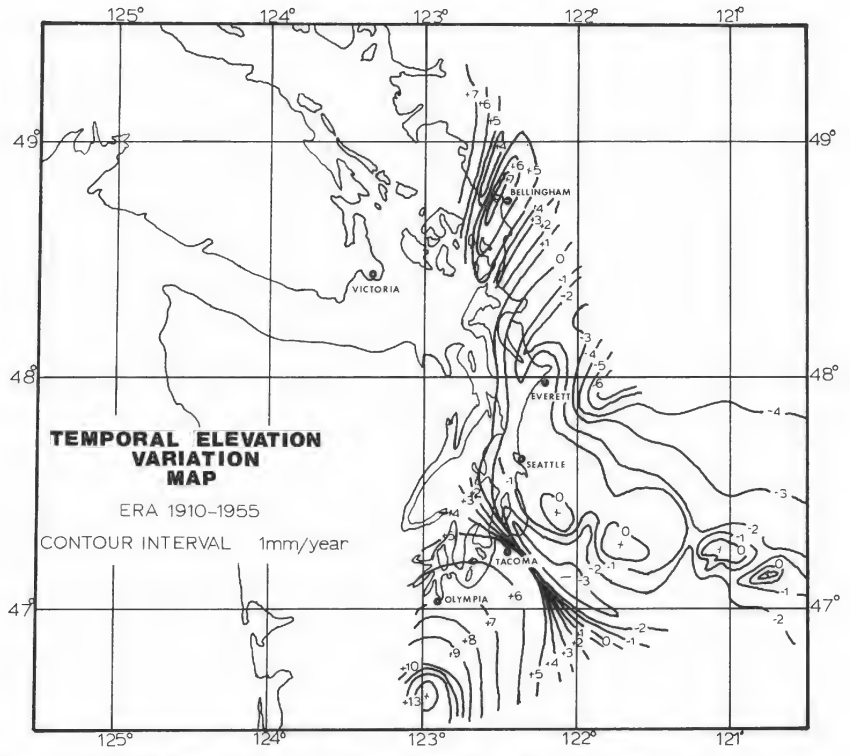


Figure 1. Temporal elevation map of the Puget lowland, Washington (atfer Couch 1970).

the Eocene sedimentary bedrock near Renton (Fig. 2). The intrusions were probably emplaced at shallow depth (Mullineaux 1965) and are of uncertain age.

A 30-m-thick mass of dacite porphyry is exposed at a quarry about 2 km south of Orting (Fig. 2). The base of the porphyry is not exposed and, at present, outcrops are unconformably bounded by Pleistocene deposits. Xenoliths are composed of material that may have been derived from formations of late Eocene age (Gard 1968). The light grey, hornblende porphyry is conspicuously different from the other intrusive rocks in the area (Gard 1968). Columnar jointing at the periphery of the quarry and massive jointing near the center of the exposure suggest that the rock was emplaced at shallow depth (Gard 1968).

Unconsolidated Deposits

Recent regional studies of the tectonics of the Puget lowland have indicated probable continuing activity (Couch 1970, Crosson 1972-1978, Wilson *et al.* 1979, Yount and Gower 1981). If, in fact, the tectonic activity is ongoing, it can reasonably be assumed that careful study of the present morphology and the Quaternary stratigraphy may yield evidence of the underlying structure.

The Quaternary sediments were deposited during multiple major glaciations and associated nonglacial intervals (Crandell *et al.* 1958, 1965). The current terminology

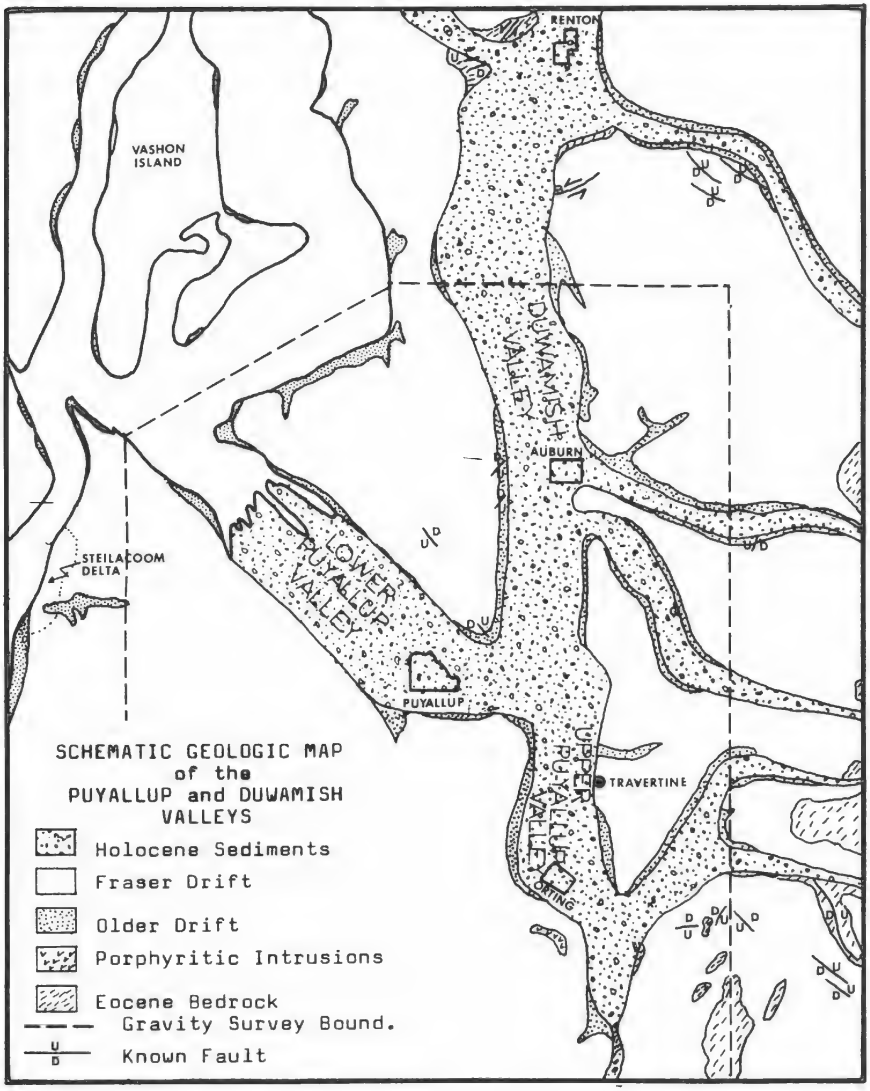


Figure 2. Generalized geologic map of the southeast Puget lowland, Washington.

for the late Quaternary geologic-climate units encountered in the southern Puget lowland region are as follows, from youngest to oldest (modified from Armstrong *et al.* 1965):

Holocene Interglaciation
Fraser Glaciation
Olympia Interglaciation
Salmon Springs Glaciation

Because of the complexity of the depositional environments, the absence of dependable correlation criteria, and the limitations of carbon-14 dating, considerable uncertainty exists concerning the proper age and lateral extent of sediments deposited prior to and during the Olympia Interglaciation. For these reasons, this paper refers to sediments deposited prior to the Fraser Glaciation simply as "older sediments."

Deposits from the Fraser Glaciation are widespread and relatively well exposed. Therefore, the depositional history is more easily understood than that of earlier glaciations. Glacial ice advanced into the southern Puget Sound about 15,000 C^{14} yr. B.P. (Mullineaux *et al.* 1965) and remained near Seattle until about 13,500 C^{14} yr. B.P. (Rigg and Gould 1957). During the recession of the glacial ice, large deltas, including the Steilacoom Delta (Fig. 2), were deposited within the large lake which formed due to ice damming the Strait of Juan de Fuca. Bretz (1978) first recognized that the topset beds of the Steilacoom Delta are at an unusually high elevation when compared to other nearby deltas that were most likely deposited in the same lake. Originally, Bretz attributed this discrepancy to a western re-advance of the Fraser ice sheet, which blocked the initial outlet of the lake. More recent studies have failed to substantiate any re-advance of the Fraser glacier (Garling 1965, Thorson 1980).

Isostatic rebound may account for a portion of the difference in elevation; however, a recent study of the isostatic effects from the last glaciation indicated a higher than expected deviation or inflection from the net post-glacial deformation which was expected for this area (Thorson 1979).

Geomorphology

The more striking geomorphologic features of the study area are the north-south trending Duwamish Valley and the northwest-southeast trending lower Puyallup Valley (Fig. 2). Both valleys were once a part of the Puget Sound marine embayment prior to their filling by marine and fluvial sediments; up to a 160 m thickness is reported in the lower Puyallup Valley (Walters and Kimmel 1968).

The Puget Sound troughs, including the valleys noted above, are thought to be primarily the result of glacial scour (Crandell *et al.* 1965). Glacial scour presumably explains the general north-south trending direction of the present marine embayments and the morphology of the Duwamish and upper Puyallup Valleys. Additional hypotheses, however, may be required to explain the origin of the lower Puyallup Valley.

As reported by Crandell *et al.* (1965), fluvial and lacustrine fill was deposited to an elevation of 45 m above present sea level due to the advancing Fraser ice. This hypothesis subsequently requires erosion by continental ice of between 200 to 250 m of sediment in the Duwamish and upper Puyallup Valleys, and 250 m in the lower Puyallup Valley. Recent studies on glacial dynamics and erosion of continental ice sheets suggest that glaciers may not have such erosive capability (Shaw 1971, Boulton 1974, Linden 1975, Whillans 1978), and there may be some question regarding the ability of continental ice sheets to erode and transport the sediments that would be required for ice scour to be the sole mechanism for forming the Puget Sound troughs. Additional questions arise regarding the origin of the Puget troughs when considering the northwest-southeast trending Puyallup Valley. The streamlined topography north and south of the lower Puyallup Valley is a strong indicator that ice flowage was in a north-south direction. Therefore, it is postulated that deep glacier scour, on the order of 150 m below

present sea level (total excavation about 250 m) in a direction not aligned with the regional trend of ice flowage is unlikely.

It is possible that the Puyallup River was entrenched in the same location prior to the advance of the Fraser ice sheet and that no significant modification occurred from the advancing glacier. Alternatively, the Puyallup Valley may be tectonically controlled, or may have resulted from a combination of the above possibilities.

Structure

Several episodes of faulting have been documented in the study area. The fault zones (Fig. 2) to the southeast and to the north appear to form two distinct sets of faults (Gard 1968, Millineaux 1965): high angle reverse faults, and normal strike faults that parallel bed fold axes. The strike faults trend north-northwest and are commonly upthrown on their east sides. The high angle reverse faults trend east-northeast and cut across the strike faults where they occur together. The relationship of the strike slip fault south of Renton to the other faults is not known. Most of these faults appear to be related to the folding of the bedrock formations.

There are four known displacements of Quaternary sediments in the area, and all occur north and west of Sumner and Auburn (Gower 1978). The two faults which occur west of Auburn (Fig. 2) trend northeast, with the upthrown block occurring on the south side. The northern fault of the two has been documented to offset the Fraser drift (Waldron 1961).

A third fault is exposed just northwest of Sumner (Crandell 1963). This nearly vertical fault trends northwest-southeast and displaces about 24 m of the Fraser drift, with the downthrown block on the south side.

Another northwest-southeast trending fault was recently discovered about 10 km north of Puyallup (Fiksdal, pers. comm., 1977). The west block has been upthrown an unknown amount.

Seismic profiling of the sediments in Commencement Bay has yielded possible evidence of post-Fraser faulting (Rogers 1970). However, seismic profiling by the U.S.G.S. has failed to confirm these displacements (Othberg, pers. comm., 1978).

When compared to other localities within the Puget lowland, there appears to be an unusually high frequency of post-Fraser displacements occurring within this area. Additional conclusions regarding whether these post-Fraser faults reflect a deep seated structure cannot be formulated with any degree of certainty.

Travertine

A highly unusual occurrence of travertine within a Fraser recessional delta was discovered just north of Orting (Fig. 2; Crandell 1963). The occurrence of this "demonstrably post-Fraser 'hot spring deposit'" is unique in the area inasmuch as no rocks or sediments rich in calcium carbonate are known in this part of the lowland (Crandell 1963). No explanation as to a possible origin of this deposit has thus far been put forward.

Seismic Observation

Interpretation Technique

The University of Washington has been operating a multi-station telemetered seismo-

graph network in western Washington since 1970. The network is areally distributed throughout the Puget Sound basin and provides accurately located hypocenters when several of the network's stations are activated by a given seismic event (Crosson 1976). Only hypocenters that were located by a minimum of five of the stations were evaluated for this study. Earthquake epicenters were plotted on 15 minute U.S.G.S. topographic maps. The foci were collapsed onto a vertical projection plane perpendicular to the lineation proposed by Couch (1970). To further analyze the projected foci, a simple 5 km grid system was constructed over the projection plane. A circular templet, 10 km in diameter, was used to count the number of events within its boundary and reported at the center of each grid. These values were then contoured as a percentage of the total events plotted.

Results

Generally, epicenters plotted within the Puget lowland show no discernable patterns. The epicenters plotted herein, however, show an interesting lineation which trends northwest through the Puyallup Valley (Fig. 3). Southwest of this feature, earthquake activity decreases significantly. The location and trend of this lineal feature correlates well with the linear gradient of elevation change and the trend of the lower Puyallup Valley. The travertine deposit is also located on this lineation.

The earthquake foci projection plane (Fig. 4) indicates that the seismic lineation also has an apparent dip to the northeast of about 45°. The contoured projection plane (Fig. 5) indicates that the majority of events occur between 15 and 20 km deep with a trend upward toward the Puyallup Valley.

Gravity Observations

Field Work

This survey used a Worden gravity meter No. 358. The majority of gravity stations were placed at U.S.G.S. bench marks or at cross roads where elevations accurate to one foot are reported on 7½ minute U.S.G.S. topographic maps. The U.S. Coast and Geodetic Survey Normal Gravity was used for latitude corrections. Terrain corrections were omitted; those due to the distant Olympic and Cascade Mountains are on the order of 3 mgal. and are resonably uniform throughout the area. Those of local influence are less than 1 mgal. in most cases. All stations were reduced to sea level. About 300 gravity stations were measured with a resultant station density of about one station per 3.5 km^2. All field work was accomplished in the winter of 1976.

Interpretation Technique

The anomalies were interpreted in terms of simple geometrical bodies. Whenever internal inconsistency was encountered, the technique developed by Danes (1960) was used until a body adequately matched the observed gravity. The representative densities employed for interpretation were as follows (Danes 1965, Walcott 1967, Jackson 1970):

Quaternary Sediments	2.20-2.30 gm cm^{-3}
Eocene Bedrock	2.40-2.60 gm cm^{-3}
Acidic Igneous Rock	2.70-2.80 gm cm^{-3}

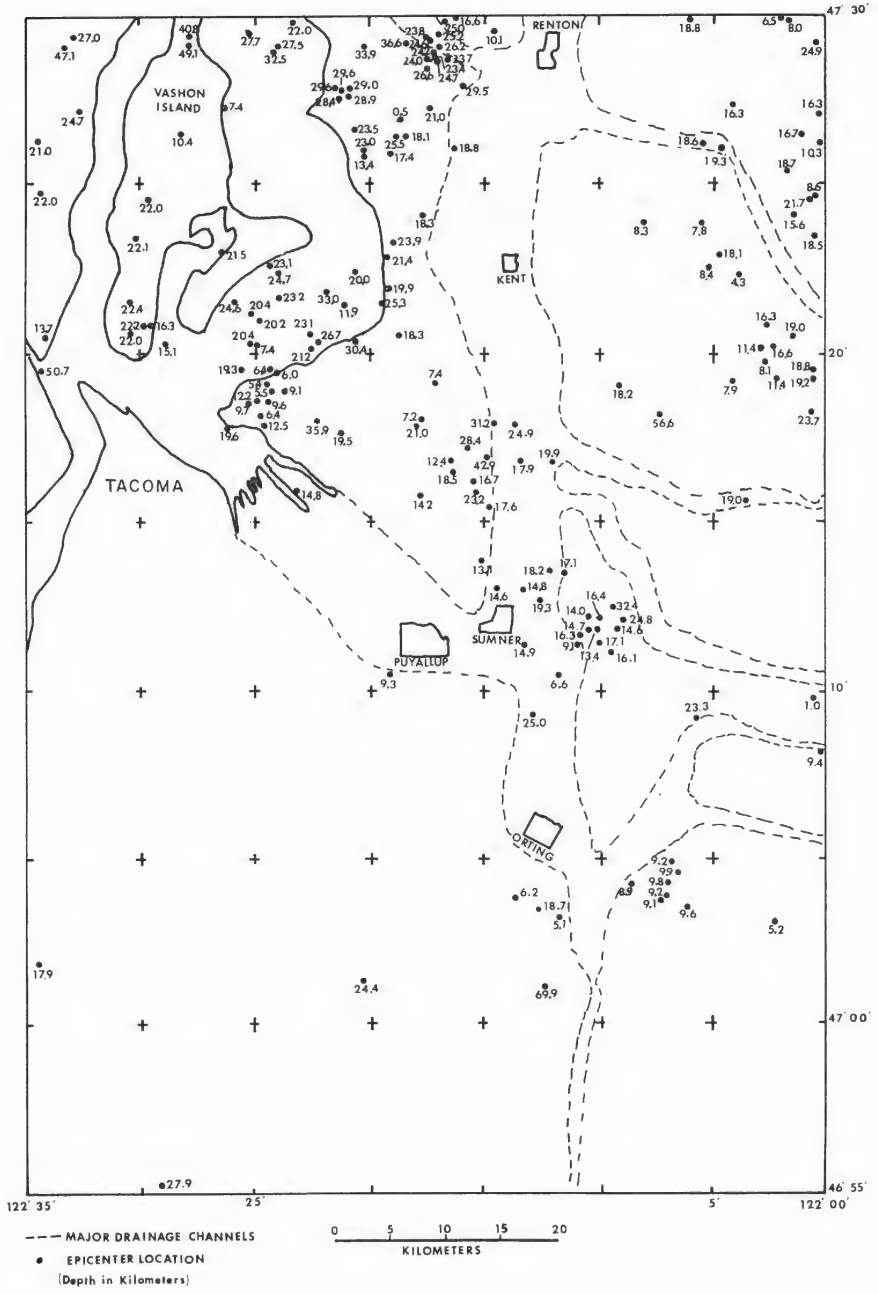


Figure 3. Earthquake hypocenter map of the southeast Puget lowland, Washington.

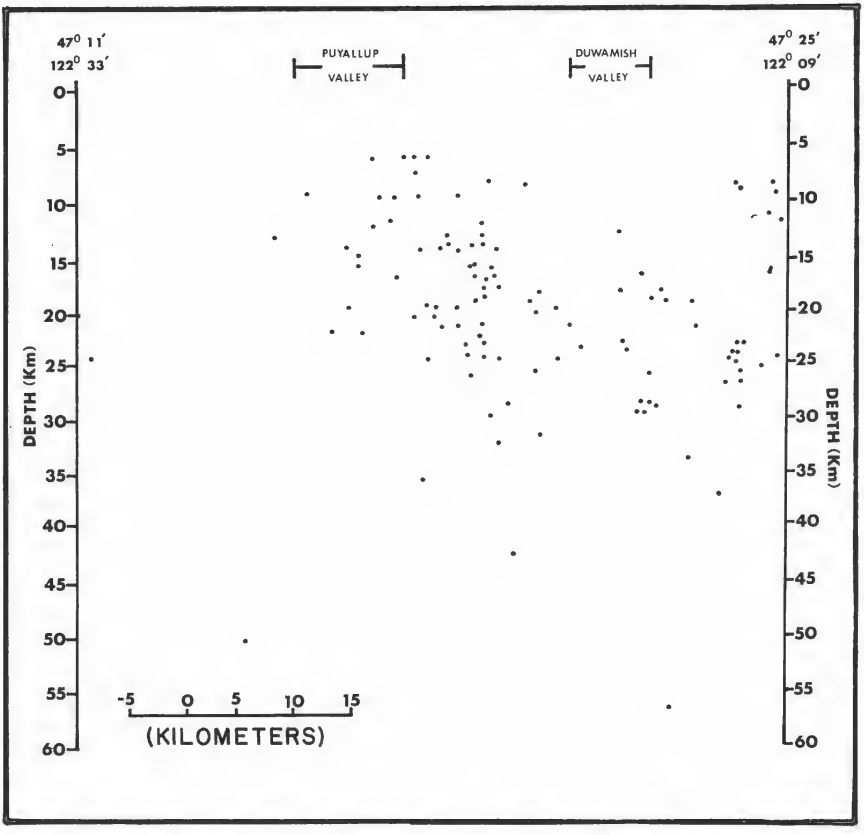


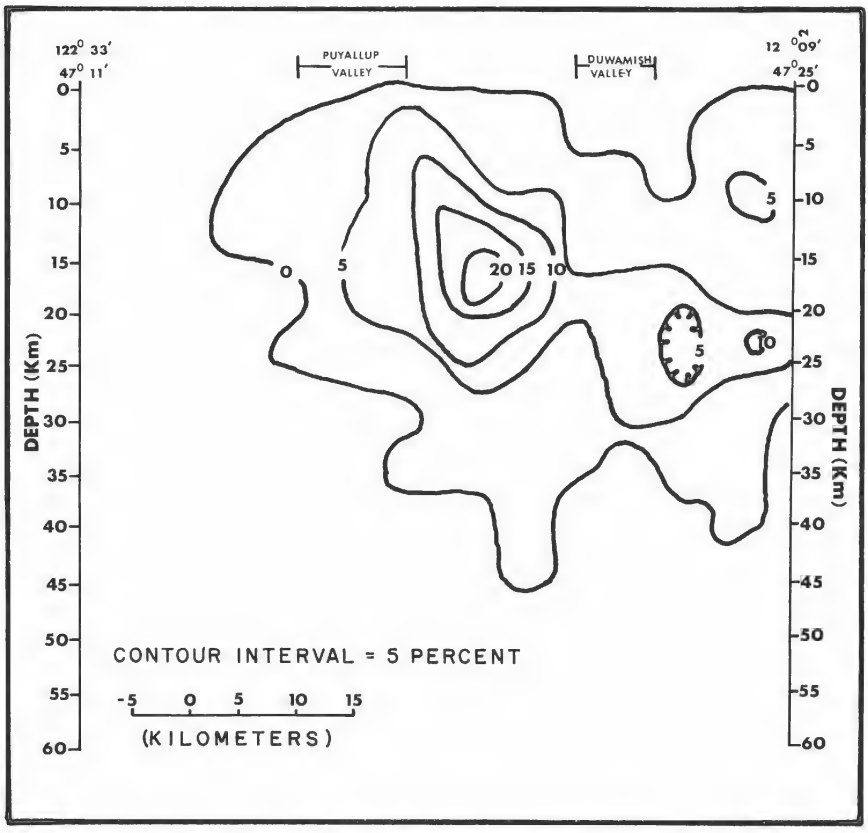
Figure 4. Earthquake foci projection plane striking N. 48° West; southern Puget lowland, Washington.

Results

The Bouguer Gravity map (Fig. 6) indicates the following prominent features:

1. Spanaway Lake Low
2. Black Diamond Low
3. Orting High
4. Puyallup High
5. Commencement Bay High

The Spanaway Lake Low corresponds to an unconsolidated sedimentary basin (Hall and Othberg 1970). The basin appears to be elongated in a north-south direction and is filled with about 600 to 1000 m of Quaternary sediments. The apparent Black Diamond Low can be best accounted for by a regional gravity decrease approaching the Cascade Mountain (Bonini *et al.* 1974) and by the expected 3.3 km thick sequence of Eocene rock occurring in this area (Gard 1968).



EARTHQUAKE FOCI CONTOURED PROJECTION PLANE

NORTH 48° WEST

Figure 5. Contoured projection plane of earthquake foci within the southeast Puget lowland, Washington.

A detailed analysis of the three gravity highs reveals that they are related and approximate a tabular shaped body, 7 km wide and 15 km deep. This tabular body trends about N. 45° W. from Commencement Bay to Puyallup and then trends about N. 15° W. from Puyallup to Orting (Fig. 6). The calculated density difference between the surrounding formations and the tabular body is about 0.20 to 0.25 gm cm^{-3}.

The Orting High appears to be closely associated with the unusual dacite exposure (Fig. 2 and Fig. 6) reported by Gard. The calculated density difference and existing magnetic data (Danes, pers. comm., 1977) further support the suggestion that the pattern of highs may represent a tabular, acidic intrusion. The location of the possible intrusion closely corresponds to the major geomorphologic features, seismic lineation, and temporal elevation changes and may represent an elongated and localized weak zone within the earth's crust which would allow the intrusion to be emplaced.

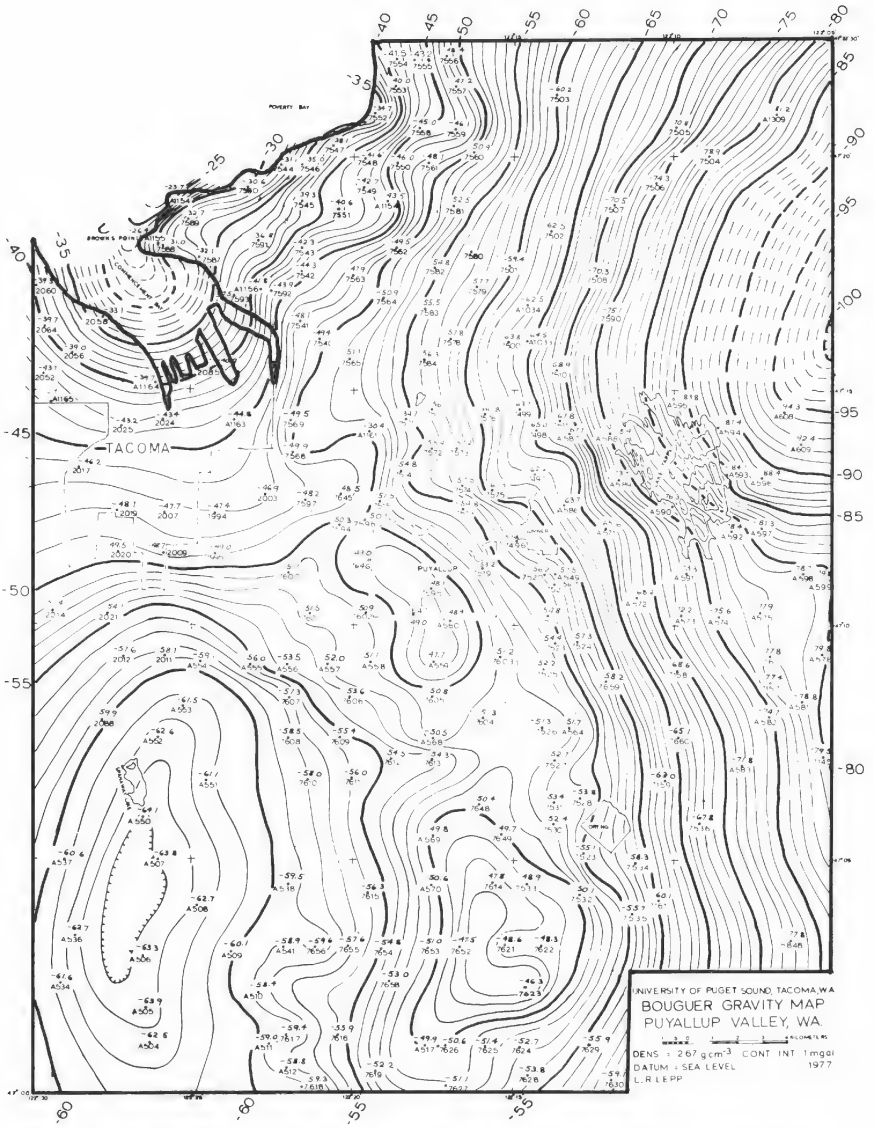


Figure 6. Bouguer gravity map of the Puyallup Valley-Southeast Puget lowland, Washington.

Discussion

Although the present investigation was unable to provide direct evidence of an active fault in the vicinity of Couch's lineal temporal elevation gradient, it is the opinion of this author that the conspicuous agreement among the various types of data—i.e., a) temporal elevation changes, b) seismic activity, c) gravity high anomalies, and d) trend of the lower Puyallup Valley—cannot be ignored. The presence of a recently

active fault or fault zone within the Puyallup Valley may also explain the travertine deposit, the elevation of the topset beds within the Steilacoom delta, the inflection of the isostatic rebound profile, and the high occurrence of Quaternary age faulting noted within the area. The data presented herein would suggest additional study would further the understanding of the tectonics of the Puget lowland region.

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Seedling Variation among Alberta Populations of White Spruce (Picea glauca (Moench) Voss) in Controlled Environments[2]

Abstract

Seedlings of 27 sources of white spruce (*Picea glauca* (Moench) Voss) were used to investigate the nature and amount of genetic variability of white spruce in Alberta. Seedlings were grown in containers for two growing seasons, in a factorial design, under two controlled environment regimes simulating northern and southern Alberta forest conditions. Of 12 characters measured, only total and top relative dry matter and number of branches were found to have significant among-source variation. Northern Alberta sources had significantly higher total and top relative dry matter than all other sources tested in both environments. Sources from central and north-central Alberta had significantly more branches than all other sources tested.

Relative dry matter increased continuously with latitude and elevation of the source. Number of branches exhibited a grouped pattern of variation. It is possible that the patterns of variability illustrated in this study could have developed from the retreat and reestablishment of white spruce in central and north-central Alberta during the late post-glacial period.

Introduction

White spruce (*Picea glauca* (Moench) Voss), one of the most widely distributed conifers in North America, grows naturally on a variety of sites throughout the boreal forest of Canada and the northern United States (Nienstaedt 1957, Nienstaedt and Teich 1972, Nienstaedt 1968). Rangewide studies have suggested clinal patterns of genetic variation in several characters (Miksche 1968, Wilkinson *et al.* 1971, Khalil 1974). While there have been studies of genetic variation and differentiation in British Columbia (Roche 1969) and Ontario (Teich and Holst 1974, Teich *et al.* 1975), there have been no similar studies in Alberta.

The objectives of this study were to determine (1) the amount of variability of selected seedling characters among populations of *P. glauca* in Alberta, and (2) any patterns of variability with respect to environmental parameters.

Methods and Materials

Controlled environment chambers were employed to simulate natural environments. Twenty-seven sources of white spruce seed, selected from the Alberta Forest Service seed bank to provide altitudinal and latitudinal gradients (Fig. 1a), were planted in

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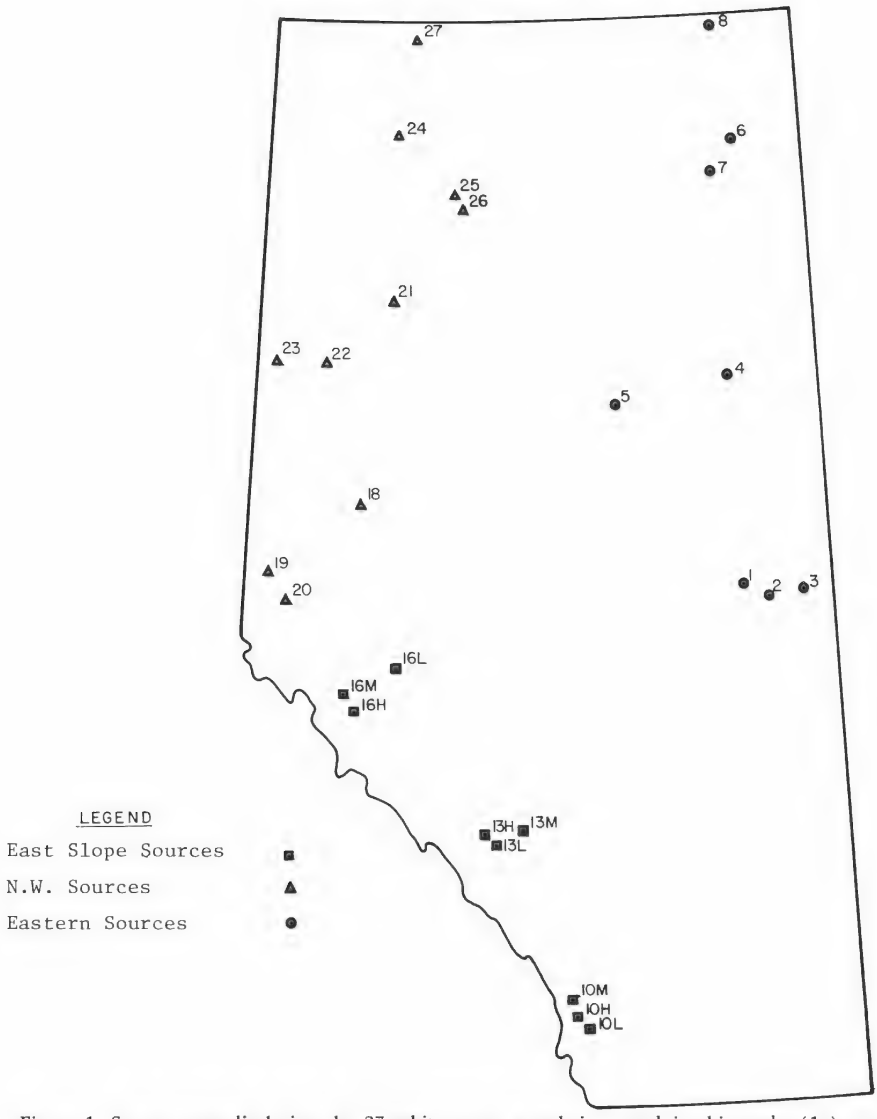

Figure 1. Source maps displaying the 27 white spruce populations used in this study (1a) and Duncan's Multiple Range Test results for total relative dry matter in the (1b) top relative dry matter (1c) and number of branches (1d) in the southern environment (dark squares are significant ($P \leq 0.05$) different from dark circles).

a factorial design in each of two growth chambers and grown for two simulated growing seasons. The factorial design of this experiment consisted of two environments with three replicates per environment, and six seedings per population in each replicate. Analyses were carried out using replicate means for a given character. Missing values were accounted for in the analysis of variance using a weighted average approach.

The twenty-seven sources were grown in Spencer Lemaire (Ferdinand) containers throughout the study period. The initial soil medium was pure peat. Regular watering, approximately twice a week, began four weeks after seeding. The seedlings were fertilized biweekly with nutrient solution (approximately 1 litre per tray of 112 p.p.m. N, 69 p.p.m. P, 156 p.p.m. K). Six weeks before the end of each growing season, regular waterings were reduced to once a week or whatever was just sufficient to keep the seedlings from wilting. At this time, a hardening-off solution of 32.87 g of 10-52-10 (N-P-K) in 40 litres of water was used biweekly in place of the regular nutrient solution until the end of the growing season.

The two growing seasons used as test treatments simulated the photoperiod, day-night temperature, and relative humidity of northern and southern Alberta growing seasons. Simulations were based on data from Ft. Smith, N.W.T., and Pincher Creek, Alberta, meteorological stations (List 1966, Anonymous 1968, Anonymous 1971). Conditions were altered every two weeks to simulate the progression of growing seasons (Dunsworth 1977).

During both growing seasons, individual height measurements were carried out biweekly. Between growing seasons the seedlings in each environment were subjected to 10 weeks of 4°C day-night temperatures (with some supplementary lighting) as a treatment to break dormancy (Nienstaedt 1966, 1967). At the end of the second growing season, final height, diameter at first internode, and number of branches were taken. The seedlings then were destructively sampled to determine total fresh weight, total dry weight, top fresh weight, top dry weight, fresh weight root-to-shoot ratio, dry weight root-to-shoot ratio, top dry weight to top fresh weight ratio (top relative dry matter), and total dry weight to total fresh weight ratio (total relative dry matter). The latter two measures are estimators of succulence or the degree to which the plant has withdrawn water from its tissues during the hardening process. Langlet (1959, 1967) has indicated that dry matter percentage (relative dry matter) is well correlated with length of growing season and latitude of the provenance for Scots pine in Sweden. Relative dry matter indicates the plants' adaptation to temperature and day length of the native habitat of the provenance.

The analyses of the data were carried out in two sections:

1. First season results:
   a) analysis of variance (ANOVA) of final first season heights;
   b) correlation analyses of first season heights on environmental parameters (latitude, longitude, elevation, and latitudes adjusted for elevation (Wiersma 1964)).

2. Final results:
   a) ANOVA of second season height growth and all final measurements;
   b) correlation analysis of measurements showing statistical significance ($P \leq .05$) among sources within treatments using environmental parameters as independent variables;
   c) Duncan's Multiple Range Test of measurements showing ANOVA statistical significance ($P \leq .05$) among sources within treatments;
   d) principal components analysis using all final measurements.

First Season Results

Analysis of variance of seedling heights at the end of the first growing season indicated a significant ($P \leq 0.001$) difference between treatments (simulated northern and southern environments). However, no significant differences could be detected among sources within treatments. There were no significant correlations of first season final heights on latitude, longitude, elevation, and converted latitudes in either growth regime.

Analysis of growth at biweekly intervals (expressed as a percentage of first season final height) using analysis of variance indicated that significant ($P \leq 0.001$) differences existed among biweekly growth periods in both environments. However, no significant differences were evident among sources within either environment.

Second Season Results

Analysis of variance of all final measurements indicated that there were significant ($P \leq 0.05$) differences among sources with respect to three measures: total relative dry matter or the ratio of total dry weight to total fresh weight, top relative dry matter or the ratio of top dry weight to top fresh weight, and number of branches per individual (Dunsworth 1977). Correlation analysis of the above characters with respect to environmental parameters indicated that these were also the only variables with any significant ($P \leq 0.10$) correlations (Table 1; Dunsworth 1977).

TABLE 1. Summary table of correlations of total and top relative dry matter and number of branches versus latitude, elevation, and converted latitude of the source(27 sources of white spruce grown in simulated northern and southern Alberta environments).

		Latitude	Elevation	Converted Latitude
Top Relative	SE	0.54***	-0.65***	-0.49***
Dry Matter	NE	0.09	-0.41	-0.67***
Top Relative	SE	0.64***	-0.62***	-0.25
Dry Matter	NE	0.35*	-0.47**	-0.34*
Number of	SE	0.04	0.12	-0.50***
Branches	NE	-0.04	-0.10	-0.19

SE—Southern Environment
NE—Northern Environment

* $P < 0.10$
** $P < 0.01$
*** $P < 0.001$

Analysis of all final measurements indicated that three principal components accounted for a significant (eigenvalues ≤ 1.0; Isenbrands and Crow 1975) proportion of the variation among sources within either environment. In the northern and southern environments, ordering of principal components was the same. The first principal component was essentially an overall size component, the second a root-to-shoot ratio component, and the third a relative dry matter (hardiness) component. Within the northern and southern environments, the first two principal components accounted for 84.5 and 86.4 percent, respectively, of the inter-source variation.

The 27 white spruce sources tested have coefficients of variation (C.V.) for total and top relative dry matter ranging from 5.8-8.0 percent (Dunsworth 1977). The greatest amount of variability existed in total relative dry matter. The poor performing high elevation sources (10H, 13H, 16M, 16H) tended to have larger than average coefficients of variation (ranging from 4-18 percent).

With respect to number of branches, the 27 white spruce sources had coefficients of variation of 20.4 and 23.8 percent, respectively, in the northern and southern environment. Thus, numbers of branches appear to have greater standard deviations relative to their means than do total and top relative dry matter. Although these different variables were measured in different ways, it appears that greater variability exists among the white spruce sources for number of branches than for total or top relative dry matter.

The correlative trends between environmental parameters and total and top relative dry matter differed only slightly between environments. Both tended to decrease with increasing elevation and increase with increasing latitude of the source (Figs. 2, 3, 4, 5). These consistent relationships were not evident with number of branches (Table 1).

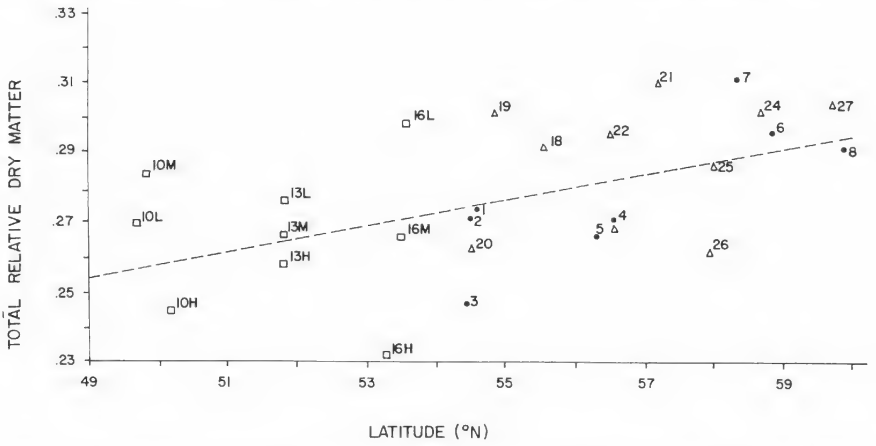

Figure 2. Relationship of total relative dry matter and latitude of 27 white spruce sources grown in a simulated southern Alberta environment ($r = 0.537$, $y = 0.074 + 0.0037\ x$).

Analysis by Duncan's Multiple Range Test of total and top relative dry matter, as well as number of branches, showed some significant ($P \leq 0.05$) groupings of sources in both environments (Figures 1b, 1c, 1d).

Total and Top Relative Dry Matter

In general, relative dry matter measure (hardiness) tended to increase in both environments as latitude of the source increased. The relationships in the southern-type environment were more significant than the same relationships in the northern-type environment.

Relative dry matter of all sources tended to decrease with increasing elevation. The plants in the southern environment tended to have more significant relationships with elevation than those in the northern environment. This elevational relationship appears to contradict the latitudinal relationship previously discussed. One would logically assume that higher elevation sites would be climatically similar to higher latitude sites. Thus, the trends with respect to latitude and elevation would be expected to parallel each other. One possible explanation for the apparent anomaly reported herein is that the photoperiodic change caused by displacement in latitude may be more influential than displacements in elevation when considering relative dry matter (hardiness). This

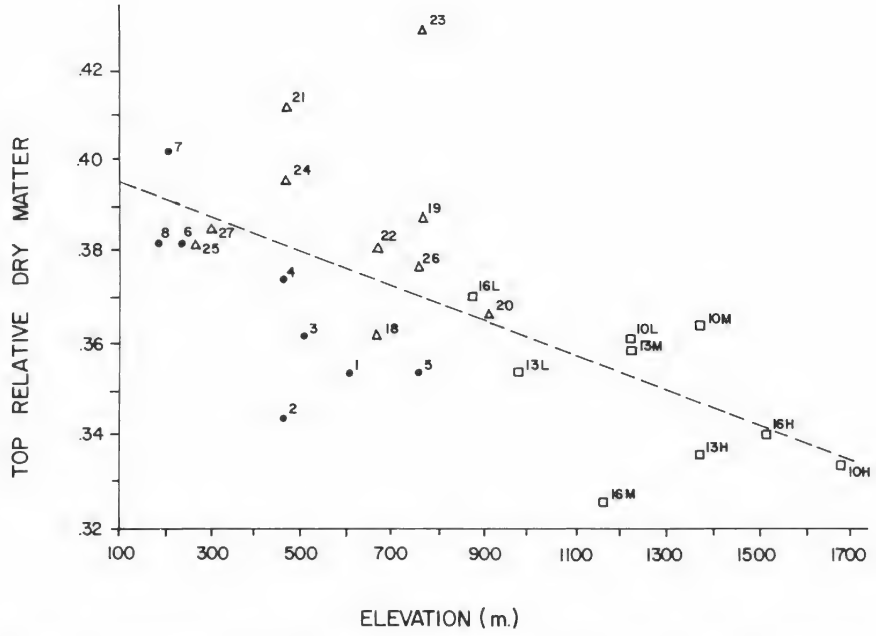

Figure 3. Relationship of top relative dry matter and latitude of 27 white spruce sources grown in a simulated southern Alberta environment ($r = 0.644$, $y = 0.085 + 0.0052\ x$).

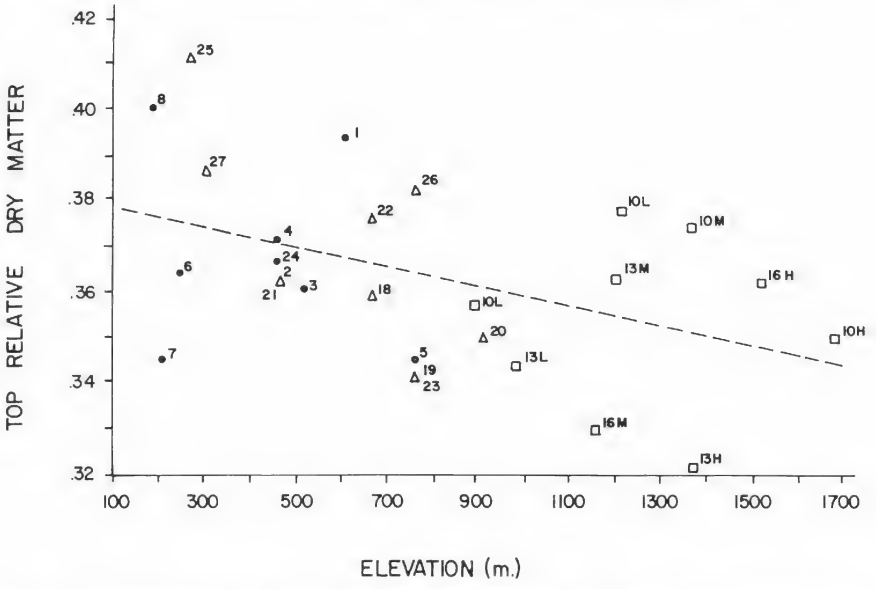

Figure 4. Relationship of top relative dry matter and elevation of 27 white spruce sources grown in a simulated northern Alberta environment ($r = 0.496$, $y = 0.38 - 0.00002\ x$).

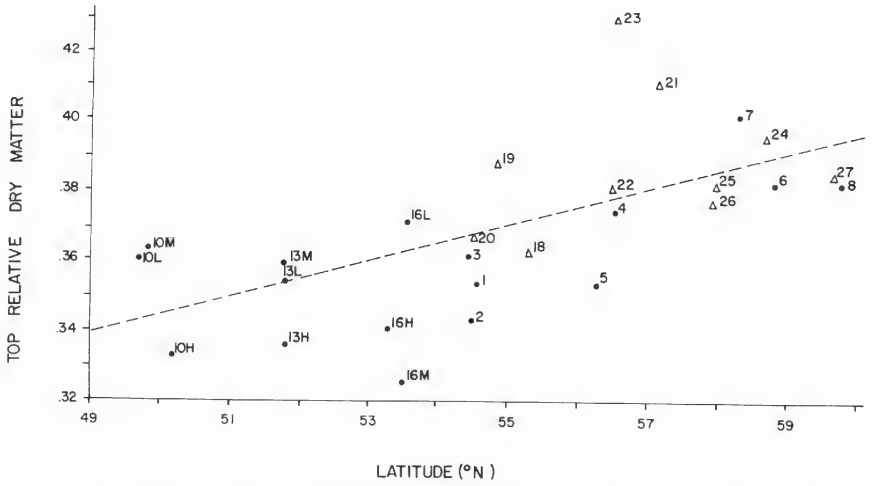

Figure 5. Relationship of top relative dry matter and elevation of 27 white spruce sources grown in a simulated southern Alberta environment ($r = -0618$, $y = 0.396 + 0.000035\ x$).

conjecture, together with the fact that there is a very strong inverse relationship between latitude and elevation of the sources used in this study ($r + -0.871$, $P \leqq 0.001$), would lead one to believe that the elevation trends probably confirm the strong influence of latitude of the source on relative dry matter. (Also see Figs. 1b, 1c).

In all but one case (total relative dry matter in the northern environment), northern sources have significantly higher total and top relative dry matter than do southern sources. In the exceptional case, total relative dry matter in the northern environment, a number of northeastern sources and two extreme southern sources have significantly higher relative dry matter than any of the other sources.

In general, considering only total relative dry matter rankings, those sources with high rankings in the simulated northern environment tended to have much lower rankings when grown in the simulated southern environment. Only three sources (numbers 8, 21, and 22) of the top 10 in the simulated northern environment remained in the top 10 in the southern environment. Of these, only one (source 8) remained in the group with the significantly highest total relative dry matter values. With respect to top relative dry matter, those sources which performed best in the northern environment tended to perform poorly in the southern environment. However, this change in performance was not nearly as evident as it was in the total relative dry matter measures. Five of the top 10 sources (numbers 8, 22, 24, 25, and 27) from the northern environment remained in the top 10 in the southern environment. Of these, four sources (numbers 8, 24, 25, and 27) remained in the group with the significantly highest top relative dry matter.

The poorest performers with respect to both total and top relative dry matter in both environments were high elevation sources (numbers 10H, 13H, 16M, and 16H). These sources remained in the bottom 10 in all cases and tended to have greater than average variability.

Number of Branches

Among-population differences in number of branches tended not to be as significant as total or top relative dry matter, nor was the pattern of variability as well defined. Specifically, when considering all sources, number of branches showed a significant ($P \leq .05$) correlation only in the southern environment with respect to converted latitudes. Number of branches for the northwestern sources were significantly ($P \leq .05$) correlated with latitude of the source, but only in the southern environment. In both environments the number of branches on the eastern sources was significantly ($P \leq .05$) correlated with latitude of the source. These results indicate that a weak but noticeable trend exists for number of branches to decrease as latitude of the source increases, particularly under simulated southern Alberta conditions.

The pattern of variability with respect to number of branches and latitude can be further illustrated by the results of Duncan's Multiple Range Test. Source maps of significantly different groups of sources from either environment indicated that a group in the central and north-central region of the province tended to have significantly higher numbers of branches than sources to the north or south of this area (Fig. 1d).

In terms of rankings it generally appears that sources which perform well under northern environmental conditions (i.e., those with high numbers of branches) perform as well or better under southern environmental conditions. Six of the top 10 sources under northern environmental conditions (sources 1, 2, 3, 5, 16L, and 19) remained in the top 10 in the southern environment. However, only two sources (sources 1 and 15) remained in the group with a significantly greater ($P \leq .05$) number of branches. Both northern and southern sources (i.e., sources 8, 10M, 13L, and 21) were consistently poor performers in both environments.

Although there appears to be a weak tendency for number of branches to decrease as one moves from the central portion of the province northward, the more significant relationship appears to be the greater number of branches exhibited by sources in the central and north-central region of the province relative to all others tested. This group of "high branch number sources" appears to be similar to the zone found by Hellum (1971) for seed weight of a number of Alberta sources of white spruce. Hellum's "central zone" extended from 53° to 57° N latitude. In the present study the "central zone" extends from about 53°-58° N latitude.

Conclusions

If one can assume, as Langlet (1967) has, that autumnal relative dry matter essentially reflects winter hardiness, it appears that the northern Alberta sources of white spruce tend to be more hardy than any of the other sources tested. The hardiness of northern sources may well be explained by the strong relationship between relative dry matter and latitude of the source. Changes in latitude correspond to changes in photoperiod. Lavee (1973) hypothesized that photoperiod is the most important environmental trigger involved in the initiation of dormancy. The initiation of dormancy and the subsequent increase in dry matter are two of a number of processes involved in a plant's preparation for winter. If photoperiod is a major trigger in these processes, northern sources (adapted to the longer days of the northern growing season) when grown in a southern environment should receive their trigger to harden off earlier than southern sources. Thus, by autumn, northern sources should have greater relative dry matter and more hardiness

than the southern sources. Conversely, southern sources in a northern environment will receive their short photoperiod trigger later than northern sources. Consequently, northern sources would again tend to be hardy earlier than southern sources.

The low and considerably variable relative dry matter of the high elevation, east-slope sources may be explained by a unique set of selective forces at work at these high elevations. These sites tend to have a greater seasonal variability in environmental conditions. Severe drought conditions during the growing season, stress due to exposure, poorly developed soils, and occurrence of warm temperatures for short periods during winter prevail on these higher elevation sites. It is feasible that these factors, as selective forces, have had a greater influence on the survival of white spruce at higher elevations than has winter hardiness. The reduction in selective importance of winter hardiness may have led to lower and more variable autumn dry matter than for spruce from lower elevations.

The pattern of variation in number of branches is not similar to that of total or top relative dry matter and does not show similar, significant relationships with any environmental parameters. However, the preponderance of sources with more branches in the central and north-central region of the province appears similar to the pattern of variation in seed weight which Hellum (1971) illustrated. Possibly, the selective forces which have acted to shape the pattern of variation for seed weight may be similar to those which shaped the pattern of variation for number of branches.

Grassland likely expanded into the area formerly occupied by forests of central Alberta during Hypsithermal Interval, approximately 5000 to 8000 years ago, when the climate became warmer and drier (Hansen 1949, 1952; Moss 1952, 1955). During this period, boreal species may have been eliminated from central Alberta and only persisted in the cooler and moister east-slope and northern regions of the province (Raup 1934, 1935; Moss 1952; Deevey and Flint 1967; Lichti-Federovich 1970; Ritchie 1976). Separation of these two boreal zones may have continued for 2000-3000 years. Such isolation may have permitted genetic differentiation, yielding two genetically distinct groups of white spruce near the end of the Hypsithermal. As the climate became cooler and moister, the boreal species became reestablished on the extended grassland region, which may have been a zone of genetic mixing between the two previously isolated groups of white spruce.

Selective forces acting on white spruce during the period of reestablishment would tend to favor different characteristics than those favored under the more normal late-successional situation. Lighter spruce seed would probably have a competitive advantage in this reestablishment, since they would expectedly disperse farther, and could become established more quickly at greater distances than would heavy seed. Relatively open sites, which would likely have been prevalent in the region of reestablishment during the post-Hypsithermal period, would likely have favored individuals with more branches and fuller crowns, since they would probably be more photosynthetically efficient.

Total and top relative dry matter, on the other hand, exhibit continuous variation with no noticeable discontinuities in the northcentral region. It may be possible that during the separation of the boreal zones, selection for plants able to become frost hardy (i.e., high relative dry matter) early in the growing season continued in the two groups. It is also feasible that during and since the post-Hypsithermal period this same

selective force has persisted. If this hypothesis is correct, then the outcome would likely have been a continuous pattern of variation in autumn dry matter relative to latitude. Thus, it may have been possible for a variety of selective forces, acting on a number of characters, to shape the differing patterns of variation illustrated in this study.

Acknowledgments

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Editor's Note

At the October 1982 Board meeting of the Association, the Trustees approved the creation of three new editorial posts: chemistry and physics, engineering and mathematics, and the social sciences. We welcome contributions from these areas.

Beginning with this issue, papers published in *Northwest Science* will be indexed in *Current Contents*. Appearing weekly, *Current Contents* reaches more than 200,000 readers.

The last cumulative author bibliography and subject index published by *Northwest Science* spanned the 26 years 1947-1962 (M. P. Kinch, compiler); this index is available from the Treasurer for $4. An index from 1973 through 1982 is in preparation, and we hope to have it printed by year's end. Announcement of its availability will be made in these pages. In addition, *Northwest Science* plans to publish a yearly index henceforth.

Errata

Hanley, T. A. Cervid activity patterns in relation to foraging constraints: western Washington pp. 208-217 Northwest Science 56(3).

Page 209: Change –5°C and –20.6°C in line 5 under Study Area to 23°C and –5°C, respectively.

Northwest Science

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The pages of *Northwest Science* are open to scientists in the basic, applied, and social sciences wherein original or fundamental research is presented. *Northwest Science* does not publish notes, letters, or bibliographic papers. Short papers are treated the same as longer manuscripts. All submissions are refereed, usually by two reviewers. Papers are also welcome from authors outside of the Pacific Northwest.

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Population Estimates and Size Regimes of Cutthroat and Brook Trout in Diamond, Kendall, and Spring Creeks, Idaho

Abstract

Population estimates of size regimes were determined for cutthroat (*Salmo clarki*) and brook trout (*Salvelinus fontinalis*) populations during 1976 and 1977 at Diamond, Kendall, and Spring creeks, Idaho, to determine if these streams are extensively used as spawning grounds and rearing areas for the Blackfoot River and Blackfoot Reservoir trout fishery. Spring and Kendall creeks supported the largest tout densities, totaling over 4780 and 2264 fish/km. Three stations were sampled on Diamond Creek, of which only Station 1 consistently contained over 1000/km. Stations 2 and 3 had low trout densities and were affected by cattle grazing.

Reproduction was observed in November 1976 at all three streams for brook trout, whereas cutthroat trout spawned in June and July 1977. Mean standard length values for cutthroat trout at Spring Creek were always below 100 mm. This trend of large populations of small fish was also observed at Kendall and Diamond creeks, indicating that the three streams were used as rearing grounds and spawning areas.

Introduction

The Blackfoot River and Reservoir in southeastern Idaho have been extensively fished for trout. The trout fishery in the Blackfoot River drainage includes naturally reproducing, self-sustaining populations of cutthroat and brook trout (*Salmo clarki* and *Salvelinus fontinalis*). Adults of both species spawn in tributaries of the Blackfoot River and migrate back to the Reservoir after the spawning season. The tributaries are thought to be used as rearing areas by the juvenile trout. Although the contribution of tributaries of the Blackfoot River as spawning grounds and rearing areas has not been extensively documented, other examples of the use of tributaries for this purpose by cutthroat and brook trout are well known (Raleigh 1969, Raleigh and Chapman 1971, Benson 1960, Cope 1957, Carlander 1969). This study attempts to demonstrate the value of Spring, Kendall, and Diamond creeks, Idaho, as spawning and rearing areas for cutthroat and brook trout and how, with the possible advent of mining activities in the area and continuing cattle grazing on Diamond Creek, possible damage to the spawning and rearing grounds could occur.

Description of the Area

Diamond, Kendall, and Spring creeks are tributaries of the Blackfoot River, and are

located approximately 30-40 km east of Soda Springs, Idaho, in the Upper Valley. The Diamond Creek area constitutes a complex ground water system which characteristically has water infiltrating from all three streams. Spring Creek arises from several cold springs (7°C) near Diamond Creek which, along with Kendall Creek, flows north from the mountains.

Fish were collected at three locations on Diamond Creek starting below Yellow Jacket Creek at the Forest Service border in the Upper Valley. Station 1 shows little visual sedimentation or bank degradation. Bank and pool cover also appear to be excellent. The stream flows quickly, with alternating series of riffles and pools and overhanging banks with an extensive growth of willows.

Stations 2 and 3, also on Diamond Creek, are located north of the Forest Service boundary in areas of extensive cattle grazing. Both stations were affected by grazing, which resulted in heavy silt deposition, eroded banks, stream channelization, and a slower flow. Willow stands, which were evident at Station 1, had been removed or killed in the area of Stations 2 and 3. A diversion dam located downstream from Station 2 further reduced the stream flow at Station 3. Kendall Creek (Station 4) and Spring Creek (Station 5) had less siltation and better stream conditions. Both sites had alternating pool-riffle habitats, overhanging banks, and extensive growths of submerged macrophytes in the stream, with stands of willows along the banks to provide stream cover for fish.

Methods and Materials

Cutthroat and brook trout were captured at five stations on Diamond, Kendall, and Spring creeks from August 1976 to July 1977. Sampling was performed monthly until December, when heavy snows prevented access, and resumed in May, June, and July 1977. Fish were captured with a D.C. powered electroshocker, two seines, and dip nets. Seines were used to block each end of a 100 m section of stream to prevent immigration into and emigration from the area. Fish were anesthesized with quinaldrine, and weighed and measured for standard length using a spring balance and a measuring board. All fish were released after sampling at each site was concluded.

Population estimates were determined by the successive removal technique described by Libosvarsky (1966) and Carle and Strub (1978). Fish were shocked three successive times in a closed 100 m section of stream to estimate population size of the cutthroat and brook trout by a least squares regression. Fish larger than 150 m were tagged with Spaghetti Floy tags before being released.

Sediment samples were taken in the fall from pool and riffle habitats at the three sites on Diamond Creek to determine the possible effects of siltation from cattle grazing or future mining operations on the trout populations. Sediment was collected in liter bottles and preserved with 10 percent formalin before being sieved through 8.0, 5.6, 3.36, 1.0, and 0.5 mm mesh sieves. The several groups of particle sizes were weighed on a triple beam balance to determine the percent composition of each particle size per substrate sample.

Diamond, Kendall, and Spring creeks also functioned as rearing grounds for both cutthroat and brook trout. Spring Creek cutthroat trout occurred in greatest numbers during September through December, and July, although the mean standard length never exceeded 100 mm. The mean standard length at Kendall Creek exceeded 100 mm only in September and June, which supports the idea that Spring and Kendall creeks

are supporting large populations of small trout and thus serving as rearing grounds for trout in the Blackfoot River drainage.

Sediment samples from Diamond Creek were sieved into six groups of particle sizes (Table 3). Silt accumulation was found to be greatest at Station 2 in the pool area

TABLE 1. Fish population estimates for Diamond Creek, Idaho, based on electrofishing (D.C.) from August 1976 through July 1977.

sample station	Date	Population estimate Fish/km	Size range (mm)	Percent species composition (mean standard length) Cutthroat Trout	Brook Trout
Diamond Cr.	02 Aug. 76	240	60-218	76 (118)	24 (129)
Station 1	03 Sept.	1,080	25-183	87 (119)	13 (104)
	18 Sept.	1,200	38-181	88 (109)	12 (92)
	17 Oct.	220	45-150	73 (60)	27 (125)
	19 Nov.	1,444	27-179	69 (81)	31 (92)
	16 Dec.	290	101-164	87 (124)	13 (137)
	07 April 77	197	40-163	67 (98)	33 (123)
	01 June	333	53-470	100 (218)	0
	05 July	1,020	57-209	88 (111)	12 (144)
Diamond Cr.	02 Aug. 76	260	62-199	100 (122)	0
Station 2	04 Sept.	1,140	30-173	93 (100)	7 (74)
	17 Oct.	300	38-115	100 (64)	0
	20 Nov.	183	52-139	100 (88)	0
	16 Dec.	900	34-68	100 (50)	0
	07 April 77	164	85	0	100 (85)
	01 June	191	65-480	83 (206)	17 (137)
	05 July	82	69-142	100 (107)	0
Diamond Cr.	03 Aug. 76	330	58-320	100 (111)	0
Station 3	19 Sept.	972	29-224	100 (79)	0
	16 Oct.	380	38-284	94 (71)	6 (163)
	20 Nov.	455	20-151	97 (61)	3 (79)
	16 Nov.	Frozen			
	07 April 77	Frozen			
	01 June	0			
	05 July	0			

TABLE 2. Fish population estimates for Kendall and Spring Creeks, Idaho, based on electrofishing (D.C.) from August 1976 through July 1977.

Sample station	Date	Population estimate Fish/km	Size range (mm)	Percent species composition (mean standard length) Cutthroat Trout	Brook Trout
Kendall Cr.	03 Aug. 76	820	47-233	94 (94)	6 (131)
	10 Sept.	2,264	28-205	72 (101)	28 (77)
	16 Oct.	640	30-131	91 (62)	9 (92)
	20 Nov.	1,409	42-251	87 (96)	13 (151)
	19 Dec.	759	31-150	73 (86)	27 (90)
	07 April 77	1,049	20-233	64 (83)	36 (121)
	02 June	540	37-406	85 (130)	15 (91)
	05 July	755	29-141	51 (63)	49 (51)
Spring Cr.	18 Aug. 76	660	32-165	69 (82)	31 (80)
	19 Sept.	4,780	32-150	89 (71)	11 (89)
	16 Oct.	4,660	29-130	90 (58)	10 (92)
	21 Nov.	1,703	30-195	71 (72)	29 (148)
	19 Dec.	1,344	38-168	95 (68)	5 (165)
	07 April 77	754	32-111	95 (50)	5 (103)
	02 June	683	30-400	88 (69)	12 (63)
	05 July	1,225	35-126	40 (60)	60 (79)

TABLE 3. Percent composition analysis of substrate from Diamond Creek stations determined from dried seliment weights.

Particle size (mm)	Station 1		Station 2		Station 2	
	Pool	Riffle	Pool	Riffle	Pool	Riffle
<0.5	0.1	0.02	82.6	3.9	4.2	6.3
0.5-3.36	0.1	0.06	0.1	0.7	0.5	3.8
1.0-3.36	0.4	0.6	0.2	12.2	3.0	14.2
3.36-5.6	0.3	1.5	2.7	5.9	3.8	7.2
5.6-8.0	0.3	0.5	4.3	6.2	4.6	7.2
>8.0	98.4	97.2	10.0	71.2	84.3	61.2

(82.6 percent). Riffle areas from Stations 2 and 3 also contained considerable percentages of small sized particles (less than 3.36 mm diameter) ranging from 12.2 to 14.2 percent (Table 3).

Results

Population estimates and size regimes of cutthroat and brook trout from Diamond, Kendall, and Spring creeks are presented in Tables 1 and 2. The greatest number of trout was found in Spring and Kendall creeks, with estimates reaching 4780 and 2264 fish/km. Spring Creek consistently had over 1000 fish/km, and Kendall Creek also had high population densities. Diamond Creek displayed symptoms of overgrazing, since only the September samples were greater than 1000 fish/km at Station 2. Station 3 never reached 1000 fish/km and twice did not provide any fish. Station 1, located above the cattle grazing area, contained greater than 1000 fish/km in over 40 percent of the sampilng periods (Table 1) and contained over 1400 fish/km in November.

Cutthroat trout densities were considerably greater than brook trout densities. Tables 1 and 2 show that brook trout were more common than cutthroat trout only at Station 2 in April, when only one fish was captured, and in July at Spring Creek when 60 percent of the fish caught were brook trout.

The combined size range of cutthroat and brook trout was 20-470 mm. The largest cutthroat trout re ached 470 mm, while brook trout reached 270 mm in length.

Reproduction of cutthroat trout was observed in June and July of 1977. The occurrence of the spawning run was substantiated by the high maximum standard length values of fish from Diamond, Kendall, and Spring creeks in June (Tables 1 and 2). Mean standard length values for brook trout were greatest in November and December, corresponding to the spawning of brook trout during that time. All three creeks were used extensively for spawning sites by both species.

Discussion

This study attempted to ascertain the use of Spring, Kendall, and Diamond creeks, Idaho, as spawning grounds and rearing areas for cutthroat and brook trout. Determination of spawning grounds and rearing areas is important if management practices are to be effective in preserving the naturally reproducing, self-sustaining populations of trout for angling. The use of streams as spawning and rearing areas by lake dwelling salmonids is not uncommon. Raleigh (1969) and Raleigh and Chapman (1971) indicated cutthroat fry move from natal gravel to rearing areas in Yellowstone Lake tributaries. Brannon (1967) and Raleigh (1967) documented similar findings for sockeye salmon. The

cutthroat trout population at Diamond, Kendall, and Spring creeks consists of juvenile fish. The large number of fish with low mean standard length values (Tables 1 and 2) supports the belief that these streams are being used as rearing areas. Also, large adult cutthroat trout occur only during the spawning season of June and July in Diamond, Kendall, and Spring creeks. The presence of spawning cutthroat trout in Diamond, Kendall, and Spring creeks was established and is represented in Tables 1 and 2 by the occurrance of unusually large fish in June and July. Similarly, brook trout were observed spawning in November 1976. Thus, all three streams are used as spawning grounds and rearing areas for both species.

Spring and Kendall creeks appear to support larger populations of trout than Diamond Creek (Tables 1 and 2), although they flow a considerably shorter distance.

Diamond Creek (Station 1) did have high trout densities during September, November, and July, although not as great as Kendall and Spring creeks. However, Stations 2 and 3 on Diamond Creek supported small numbers of trout, and at times Station 3 was devoid of fish (Table 1). The area in which Stations 2 and 3 were located was affected by cattle grazing. The banks were eroded and the stream beds were laden with silt (Table 3). Phillips *et al.* (1975) documented a 20-50 percent decrease in survival of trout fry with the introduction of sediment 1-3 mm in diameter. Station 2 had over 82 percent of the sediment in pool areas within this size range and nearly 16 percent in the riffle areas. Similarly, Station 3 had over 7 percent and 24 percent silt less than 3.66mm in the pool and riffle areas, respectively (Table 3). The presence of heavy siltation probably rendered this portion of Diamond Creek unsuitable for spawning activities. Spawning trout were observed passing through Stations 2 and 3 during June and July 1977, but no redds were located in these areas. The bank erosion and siltation also reduced bank cover at Stations 2 and 3, probably explaining the occurrence of low trout densities at these sites. Hale (1952) and Hunt (1971) indicated that reduced stream cover does correspond to lower trout densities. Thus, Lower Diamond Creek is not only unsuitable as spawning grounds but also as rearing areas for cutthroat and brook trout.

The dominant trout species in the Diamond Creek area is *Salmo clarki* (Tables 1 and 2). Brook trout outnumbered cutthroat trout only in July at Spring Creek and in April at Station 2 of Diamond Creek. The latter site had only one fish collected at that time. Tables 1 and 2 illustrate that the percent species composition of cutthroat and brook trout remained similar throughout the year. Benkhe and Zarn (1976) discussed the displacement of cutthroat trout by brook trout in aquatic systems that underwent habitat degradation. The cutthroat trout population in the Diamond Creek area does not appear to be threatened by competition with brook trout, although if severe habitat degradation occurred in all three streams, the cutthroat trout population might be replaced by brook trout. Prevention of further stream degradation and installation of stream improvement structures on Diamond Creek would not only ensure the future of cutthroat trout spawning grounds and rearing areas but would also increase the available stream habitat in which spawning and rearing could occur successfully.

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Predicting Young Ponderosa Pine Growth in the Blackfoot River Drainage, Montana[2]

Abstract

The length of time required for dominant, naturally regenerated ponderosa pine (*Pinus ponderosa* Laws.) to reach diameters at breast height (b.h.) from 0.0 centimeters (cm) to 12.7 cm (5.0 inches (in.)) was predicted as a function of site index and initial spacing. Neither independent variable explained much of the variation in the time required to reach the smaller diameters, particularly the time to reach breast height. The time required to obtain a diameter at breast height ranges from four to six years for all site indexes from 10.5 meters (m) (34.4 feet (ft)) to 22.5 m (73.8 ft.) (base age 50 years). Site index becomes a more important independent variable (higher correlation with time) as d.b.h. increases, but initial spacing does not substantially affect the diameter growth rate of trees until they are nearly 12.7 cm (5.0 in) d.b.h., within the range of initial spacings included in this study. When the data were stratified by habitat type and soil mapping unit, the number of years required to reach breast height and 5.8 cm (2.0 in) b.h. was not substantially different between the strata.

Introduction

As greater emphasis is placed on the management of second-growth forests in the Northern Rocky Mountains, foresters require additional information on stand growth and development under more intensive management regimes. For trees less than 20 years old, it is particularly difficult to extrapolate existing data from naturally developed fully stocked or overstocked stands to stands which result from early stocking control. Knowledge of young stand growth and development becomes particularly important as rotations are shortened and investments in cultural treatments are considered.

Under plantation conditions the processes of competition, suppression, and mortailty may be different from stands fully stocked at establishment (Feduccia *et al.* 1979, Oliver and Powers 1978, Tesch 1980). These differences in stand development pattern ultimately affect the characteristics of the stand available for harvest.

This study attempts to quantify the length of time for naturally regenerated, dominant ponderosa pine (*Pinus ponderosa* Laws.) trees, ranging in initial spacing from 2 x 2 m (6.5 x 6.5 ft.) to open-growth (not in competition with other trees), to reach 12.7 cm (5.0 in.) b.h.

Six linear regression equations were developed to predict the time necessary to

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reach breast height, 2.54 cm (1.0 in.), 5.08 cm (2.0 in.), 7.62 cm (3.0 in.), 10.16 cm (4.0 in.), and 12.7 cm (5.0 in.) b.h., as a function of site index and initial spacing. Data were also stratified to quantify the number of years to reach breast height and to 5.08 cm (2.0 in.) b.h. for three habitat types (Pfister *et al.* 1977) and three soil mapping units (USDA 1972).

Methods

Individual tree data collected by Tesch (1980) were used to determine the time required to reach various diameters at breast height. Sample trees were dominant, phenotypically superior trees. All sample trees were located in the Blackfoot River Drainage. To represent a broad range of stand and site conditions, four factors were identified: initial spacing class (2-2.9 m, 3-3.9 m, 4-4.9 m); 10-year age class (10-80 years); habitat type (3 levels) and soil mapping unit (3 levels).[3] These factors led to the formation of 189 (3 x 7 x 3 x 3) cells. A form of list sampling was employed until approximately three trees per cell were observed.

Age to respective diameter was determined by computing the difference between the age of the tree at ground level and the age of the tree at an inside bark equivalent to the desired diameter at breast height when an estimate of double bark thickness was added. Radial growth rates were obtained by averaging the measurements from two increment cores taken at breast height and bored at right angles to one another.

Using this technique to calculate the age to the desired diameter, young stand growth can be correlated with a site index measurement obtained on mature trees. This site index measurement should better represent the long-term productive capacity (in terms of height growth) of the site than one obtained from very young trees. Site index was determined by the use of local site curves developed by Tesch *et al.* (1980) (base age equals 50 years). To avoid problems with the estimation of site index for very young trees, Tesch's data were sorted to include only sample trees greater than 20 years old. The initial spacing of these older trees, measured in unmanaged stands, was estimated by a method developed by Tesch (1980).

Step-wise multiple linear regression procedures were used to develop equations predicting age to desired diameter at breast height as a function of site index and initial spacing. For model building purposes, data were screened to include trees which ranged in site index from 10.5 m (34.4 ft.) to 22.5 m (73.8 ft.) and estimated initial spacing from 1.5 x 1.5 m (4.9 x 4.9 ft.) to 5.5 x 5.5 m (18 x 18 ft.). Based on plots of the data, models were postulated as follows:

Age = f (site index, initial spacing, initial spacing x site index)

Age = f (1/site index, 1/initial spacing, 1/site index x 1/initial spacing)

Analysis of residuals was used to assess the final equations.

The data were sorted into 3 m (9.8 ft.) site index classes, using 12 m (39.4 ft.), 15 m (49.2 ft.), 18 m (59.0 ft.), and 21 m (68.9 ft.) as midpoints of the intervals. For each site index class the mode, range, mean, and standard deviation of the time required to achieve various diameters at breast height were calculated. Since ages are discrete interval data, the mode and range were chosen for descriptive purposes as appropriate measures of central tendency and dispersion, respectively. The mode is

[3]Habitat types and soil mapping units were selected to represent a range of potential ponderosa pine productivity classes (low, medium, high).

that datum value which occurs with the highest frequency. Arithmetic means and standard deviations were used to conduct parametric tests of significance between classes, as opposed to equivalent nonparametric tests. This switch in test procedures is one of convenience and does not influence the outcomes of various tests of hypotheses (Gaito 1972).

The mode, range, mean, and standard deviation associated with age to b.h. and to 5.08 cm (2.0 in.) b.h. were computed for each habitat type (h.t.) and soil mapping unit (SMU). The three habitat types were all in the *Pseudotsuga menziesii* series, including *Symphoricarpos albus* h.t., *Agropyron spicatum* phase (PSME/SYAL AGSP); *Symphoricarpos albus* h.t., *Calamagrostis rubescens* phase (PSME/SYAL CARU); and *Vaccinium caespitosum* h.t. (PSME/VACA). The three soil mapping units were Shooflin, Winkler, and Bignell.

Results and Discussion

Equations predicting the time required to reach various diameters at breast height are presented in Table 1. These equations represent the "best" models obtainable by stepwise linear regression procedures when fitting the two postulated model forms to the data. Final equations were selected on the basis of high R^2 values, low standard deviation about regression, and analysis of residuals. Although these may be the "best" models, because all included variables are significant, it is clear that several equations do not have "good" statistics.

The correlation between site index and age to breast height is poor. Perhaps not surprisingly, it appears that on these relatively modest productivity sites in western Montana, factors other than the long-term inherent productive potential of the site strongly influence the time it takes a dominant tree to reach breast height. For example,

TABLE 1. Equations and associated statistics for predicting number of years required to reach selected diameters at breast height.

0.0 cm b.h. (0.0 in.)			
$Y = 7.2244 - 0.1178$ (Site)			
$R^2 = .035$	% S.D.[a] = 35.1	n = 408	
2.54 cm b.h. (1.0 in.)			N
$Y = 4.6830 + 79.5635$ (1/Site) $- 48.2363$ (1/Site x 1/Ispa)			
$R^2 = .12$	% S.D. = 21.7	n = 408	
5.08 cm b.h. (2.0 in.)			
$Y = 5.4272 + 116.5166$ (1/Site) $- 49.5958$ (1/Site x 1/Ispa)			
$R^2 = .22$	% S.D. = 17.5	n = 408	
7.62 cm b.h. (3.0 in.)			
$Y = 4.8039 + 165.7065$ (1/Site)			
$R^2 = .36$	% S.D. = 16.4	n = 408	
10.16 cm b.h. (4.0 in.)			
$Y = 3.8620 + 224.3588$ (1/Site) $+ 57.3841$ (1/Site x 1/Ispa)			
$R^2 = .43$	% S.D. = 17.2	n = 407	
12.7 cm b.h. (5.0 in.)			
$Y = 6.5934 + 214.2031$ (1/Site) $- 24.2016$ (1/Ispa) $+ 584.2776$ (1/Site x 1/Ispa)			
$R^2 = .52$	% S.D. = 18.6	n = 407	
where Site = site index (m)			
Ispa = initial spacing (m)			

[a]Percentage S.D. = standard deviation about regression as percent of mean response.

on those sites where grasses and/or low shrubs coexist with seedlings, the competition for available soil moisture is intense.

As trees get older and thus larger in d.b.h., site index becomes an increasingly important variable for predicting the time to reach a given diameter at breast height. Probably as trees get larger, they are less likely to be strongly influenced by microsite factors that may mask the average long-term site potential.

The R^2 values associated with the equations increase as diameter increases, indicating that more variation in the age to that diameter is explained by the independent variables. Site index is the most significant variable in all equations. Initial spacing alone does not significantly influence diameter growth until age to 12.7 cm (5.0 in.) b.h. is predicted. It should be emphasized that the equations represent plantation-like initial spacing.

The data were originally stratified by site index classes and initial spacing classes to visualize patterns that would make model building more efficient. However, when it became clear that statistically desirable prediction equations were not always possible using the selected independent variables, the number of years required to reach the desired diameter was determind for each of four site index classes (Table 2). Using

TABLE 2. Modal number of years required to reach various diameters at breast height for 3 m (9.8 ft.) site index classes.

	Model number of years	Range	n
Years to breast height			
Site Index 12 m (39.4 ft.)	5	9	33
15 m (49.2 ft.)	4	13	139
18 m (59.0 ft.)	5	8	142
21 m (68.9 ft.)	6	8	65
Years to 2.54 cm b.h. (1.0 in.)			
Site Index 12 m	10	10	33
15 m	9*	12	139
18 m	9*	9	142
21 m	9	7	65
Years to 5.08 cm b.h. (2.0 in.)			
Site Index 12 m	14	11	33
15 m	11*	11	139
18 m	11*	10	142
21 m	9	8	65
Years to 7.62 cm b.h. (3.0 in.)			
Site Index 12 m	17*	15	33
15 m	15*	14	139
18 m	14*	11	142
21 m	11	9	65
Years to 10.16 cm b.h. (4.0 in.)			
Site Index 12 m	22*	27	33
15 m	19*	18	139
18 m	17*	13	141
21 m	16	14	65
Years to 12.7 cm b.h. (5.0 in.)			
Site Index 12 m	28*	37	32
15 m	23*	25	137
18 m	21*	15	135
21 m	19	19	64

*Significant difference between mean number of years to reach a specific d.b.h. at site index group i and $i + 3$, where $i = 12, 15, 18$. Tests of significance were performed using Cochran's Approximation for two sample t-tests with unequal subclass numbers (Snedecor and Cochran 1967).

parametric test procedures, statistically significant differences (at the 5 percent level) in mean number of years were found between site index classes at larger diameters. At small diameters, practical differences are only one or two growing seasons.

The uniform period required for dominant trees to reach breast height is interesting. This uniformity suggests that on poor sites a very favorable microsite can support

TABLE 3. Modal number of years required to reach b.h. and 5.08 cm (2.0 in.) b.h. for selected habitat types and soil mapping units.

	Model number of years	Range	n
Years to breast height			
PSME/SYAL AGSP h.t.	6	13	117
PSME/SYAL CARU h.t.	6	11	116
PSME/VACA h.t.	4	8	125
Bignell SMU	5	13	162
Shooflin SMU	6	11	136
Winkler SMU	5	8	105
Years to 5.08 cm (2.0 in.) b.h.			
PSME/SYAL AGSP h.t.	13	13	117
PSME/SYAL CARU h.t.	11	12	116
PSME/VACA h.t.	11	12	125
Bignell SMU	12	13	162
Winkler SMU	11	12	105
Shooflin SMU	11	13	136

TABLE 4. T-tests for significant differences between the arithmetic mean length of time required to reach breast height and 5.08 cm (2.0 in.) b.h. for sampled habitat types and soil mapping units.

Diameter class	t'	Growth rate implication[1]
Years to breast height		
PSME/SYAL AGSP h.t. (PSA) vs. PSME/SYAL CARU h.t. (PSC)	1.79	
PSME/SYAL AGSP h.t. vs. PSME/VACA h.t. (PV)	3.68*	PSA>PV[2]
PSME/SYAL CARU vs. PSME/VACA	1.70	
Bignell SMU (B) vs. Winkler SMU (W)	1.86	
Shooflin SMU (S) vs. Bignell SMU	0.00	
Shooflin SMU (S) vs. Winkler SMU	1.80	
Years to 5.08 cm (2.0 in.) b.h.		
PSME/SYAL AGSP h.t. vs. PSME/SYAL CARU h.t.	3.33*	PSA>PSC
PSME/SYAL AGSP h.t. vs. PSME/VACA h.t.	3.40*	PSA>PV
PSME/SYAL CARU vs. PSME/VACA	2.02*	PSC>PV
Bignell SMU vs. Winkler SMU	2.60*	B>W
Bignell SMU vs. Shooflin SMU	1.27	
Winkler SMU vs. Shooflin SMU	1.31	

*Significant differences at the 5 percent level of t' (Snedecor and Cochran 1967).

[1]Growth rate implication refers to significant differences in arithmetic mean number of years required to reach the specific diameter.

[2]> Implies greater time required.

height growth at a rate essentially equal to that on better sites. On better sites, however, where overall environmental conditions may be more favorable, location within a more favorable microsite does not increase early height growth.

The number of years required to reach b.h. and 5.08 cm (2.0 in.) b.h. on the three habitat types and three soil mapping units is presented in Table 3. Once again, while statistically significant differences do occur between strata using the arithmetic mean number of years (Table 4), particularly for the 5.08 cm (2.0 in.) b.h. diameter class, practical differences are small.

Conclusions

It appears difficult to predict the height growth of young ponderosa pine using variables that are related to the long-term productive height growth potential of the site. These results document the variability in height growth rate of young vigorous trees that exhibited no previous suppression of radial growth at ground level. This variability must be due to variables other than site index. Stratification by habitat type, which theoretically provides a measure of long-term average understory microclimate, still does not appear to account for the short-term variation in such factors as temperature or moisture availability. To quantify the height growth of young ponderosa pine precisely, independent variables must be identified that can account for the short-term variability in growing conditions. Such variables might include growing season precipitation (amount and timing) and temperature (average and extremes); understory vegetation composition, phenology, structure, and density; and animal browsing.

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Acarine Ectoparasites (Mites) of Bats of Oregon[2]

Abstract

Six hundred and ninety-eight bats, representing seven genera and twelve species, were collected in Oregon and examined for ectoparasitic mites. Thirty-one species of mites in eight families were found, including a new species of macronyssid mite on *Myotis californicus, M. evotis, M. lucifugus, M. volans, M. yumanensis, Eptesicus fuscus,* and *Lasionycteris noctivagans.*

New hosts for previously known species are: *Myotis californicus (Alabidocarpus calcaratus), M. lucifugus (Cryptonyssus desultorius), M. evotis (Spinturnix americanus), M. volans (C. desultorius, S. bakeri, S. globosus, Acanthophthirius* sp. nr. *gracilis, Pteracarus* sp. nr. *minutus daubentoni, Alabidocarpus calcaratus, Notoedres {Bakeracarus}* sp.), *Eptesicus fuscus, (Notoedres {Bakeracarus}* sp.), and *Pipistrellus hesperus (Leptotrombidium myotis).*

First records for Oregon are: MACRONYSSIDAE, *Cryptonyssus desultorius, Macronyssus longisetosus, M. macrodactylus, Steatonyssus antrozoi, S. emarginatus, S. furmani*; SPINTURNICIDAE: *Spinturnix bakeri, S. globosus*; MYOBIIDAE: *Pteracarus* sp. nr. *minutus daubentoni, P. aculeus, Acanthophthirius* sp. nr. *gracilis, A. caudatus eptesicus*; TROMBICULIDAE: *Albeckia senase, Leptotrombidium myotis, Whartonia perplexa, Loomisia univari*; LABIDOCARPIDAE: *Alabidocarpus calcaratus*; NOTOEDRIDAE: *Notoedres (Bakeracarus)* sp.

Introduction

Several papers provide information on parasitic mites of Oregon mammals: Whitaker and Wilson (1974, host-parasite list), Maser and Whitaker (1980, Heteromyidae), Radovsky (1967, Macronyssidae), Rudnick (1960, Spinturnicidae), Easton (1975, chiggers), Whitaker (1979, *Zapus trinotatus*), Whitaker and Maser (1979, *Arborimus* and *Lagurus*), Whitaker *et al.* (1979, *Aplodontia*), Whitaker *et al.* (1979, moles), and Whitaker *et al.* (1980, shrews). However, little of this information pertains to ectoparasitic mites of Oregon bats. We present information frequency and abundance of mites on the bats of Oregon.

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Methods and Materials

Bats were collected mostly by mist netting or by shooting; they were brushed over a pan and their fur was examined by means of a dissecting microscope. Mites were preserved in 70 percent alcohol, cleared in Nesbitt's solution, and mounted in Hoyer's solution.

Results and Discussion

Ectoparasites were obtained from 698 bats, representing 12 species and seven genera. Between 21 and 154 individuals of each species of bat were examined, except for *Myotis leibi* and *Lasiurus cinereus*, of which only one and five, respectively, were examined. Data on mites of bats of the genus *Myotis* are summarized in Table 1; those of species of other genera in Table 2. Thirty-one species of mites, distributed among eight families, were found. Collection data are given where new distributional records are involved. Except where noted, all specimens were collected by one of us (C. Maser).

California myotis (**Myotis californicus**)

Six species of mites were found on 31 of 94 California myotis parasitized (32.9 percent), but only two macronyssids, *Macronyssus crosbyi* and an undescribed species, were found on more than one host individual. *Macronyssus crosbyi* is often found on *Myotis* (Whitaker and Wilson 1974), and the new species, which will be described subsequently, is common on Oregon bats. The other mite species found were *Cryptonyssus desultorius, Leptotrombidium myotis, Alabidocarpus calcaratus,* and *Haemogamasus ambulans.*

Mites previously reported from *M. californicus* are *Ischyropoda armatus, Cryptonyssus desultorius, Macronyssus crosbyi, Leptotrombidium myotis,* and *Whartonia perplexa* (Whitaker and Wilson 1974, Brennan and Beck, 1956). Radovsky (1967) recorded three specimens of *Cryptonyssus* from *M. californicus* but did not have enough material upon which to make a specific identification. *Haemogamasus ambulans* had not been previously recorded on this host. The occurrence of this parasite of small terrestrial mammals on bats is considered accidental.

New distributional records: *Cryptonyssus desultorius*, 1 protonymph, Malheur Co., Cottonwood Creek, 23 August 1975. *Leptotrombidium myotis,* 9 larvae, Wallowa Co., 9.5 mi. NNE Wallowa, 12 August 1975; ±135 larvae on 4 hosts, Wallowa Co., Rockwall Spring, 11 August 1977. *Alabidocarpus calcaratus* 2 ♀, Lincoln Co., 1 mi. NE Otis, 21 August 1971. Of these, *C. desultorius* and *L. myotis* are first records for Oregon, and *A. calcaratus* had not previously been reported from *Myotis californicus.*

Long-eared myotis (**Myotis evotis**)

Sixteen of 105 long-eared myotis (15.2 percent) yielded parasites. The only species recovered were *Macronyssus crosbyi*, the new macronyssid species, and *Spinturnix americanus.*

Macronyssus crosbyi, S. americanus, and *Leptotrombidium myotis* have previously been reported from *M. evotis* (Whitaker and Wilson 1974, Andersen and Jones 1971).

Long-legged myotis (**Myotis volans**)

Of 92 bats of this species examined, 28 (30.4 percent) had mites. Most abundant

TABLE 1. Parasitic mites of six species of bats of the genus **Myotis** from Oregon.*

	Myotis californicus		**Myotis evotis**		**Myotis leibi**		**Myotis lucifugus**		**Myotis volans**		**Myotis yumanensis**	
No examined	94		105		1		154		92		46	
No. with parasites	31		16		1		52		28		21	
	No. bats	No. mites	No. bats	No. mites	No. bats	No. mites	No. bats	No. mites	No. bats	No. mites	No. bats	No. mites
Macronyssidae												
Cryptonyssus desultorius	1	1	—	—	—	—	1	1	1	1	—	—
	(1.1)	(1.0)	—	—	—	—	(0.6)	(1.0)	(1.1)	(1.0)	—	—
Macronyssus crosbi	7	14	8	28	—	—	31	158	11	110	5	6
	(7.4)	(2.0)	(7.6)	(3.5)	—	—	(20.1)	(5.1)	(11.9)	(10.0)	(10.8)	(1.2)
macronyssid n. sp.	22	61	8	29	—	—	4	11	8	34	14	100
	(23.4)	(2.8)	(7.6)	(3.6)	—	—	(2.6)	(2.8)	(8.7)	(4.3)	(30.4)	(7.1)
Spinturnicidae												
Spinturnix americanus	—	—	2	14	—	—	19	57	9	13	2	2
	—	—	(1.9)	(7.0)	—	—	(12.3)	(3.0)	(9.8)	(1.4)	(4.3)	(1.0)
S. bakeri	—	—	—	—	—	—	—	—	1	1	—	—
	—	—	—	—	—	—	—	—	(1.1)	(1.0)	—	—
S. globosus	—	—	—	—	—	—	—	—	1	1	—	—
	—	—	—	—	—	—	—	—	(1.1)	(1.0)	—	—
Notoedridae												
Notoedres (Bakeracarus) sp.	—	—	—	—	—	—	—	—	1	5	1	1
	—	—	—	—	—	—	—	—	(1.1)	(5.0)	(2.2)	(1.0)
Trombiculidae												
Leptotrombidium myotis	5	143	—	—	1	4	2	21	2	4	—	—
	(5.3)	(28.6)	—	—	(100)	(4.0)	(1.3)	(10.5)	(2.2)	(2.0)	—	—
Myobiidae												
Acanthophthirius sp. nr. **gracilis**	—	—	—	—	—	—	—	—	1	1	—	—
	—	—	—	—	—	—	—	—	(1.1)	(1.0)	—	—

TABLE 1—(Continued)

Pteracarus sp. nr. minutus daubentoni	—	—	—	—	—	—	—	—	1	1	—	—
	—	—	—	—	—	—	—	—	(1.1)	(1.0)	—	—
Labidocarpidae												
Alabidocarpus calcaratus	1	2	—	—	—	—	—	—	1	1	—	—
	(1.1)	(2.0)	—	—	—	—	—	—	(1.1)	(3.0)	—	—

*Percent hosts infested and average number of mites per infested host indicated in parentheses.

TABLE 2. Parasitic mites of six species of bats of Oregon.*

	Antrozous pallidus		**Eptesicus fuscus**		**Lasionycteris noctivagans**		**Lasiurus cinereus**		**Pipistrellus heperus**		**Plecotus townsendi**	
No. examined	21		78		44		5		33		25	
No. with parasites	8		49		21		1		5		13	
	No. bats	No. mites	No. bats	No. mites	No. bats	No. mites	No. bats	No. mites	No. bats	No. mites	No. bats	No. mites
Macronyssidae												
Cryptonyssus desultorius	—	—	1	11	—	—	—	—	—	—	—	—
	—	—	(1.3)	(11.0)	—	—	—	—	—	—	—	—
Macronyssus crosbyi	—	—	1	1	—	—	—	—	—	—	—	—
	—	—	(1.3)	(1.0)	—	—	—	—	—	—	—	—
M. longisetosus	—	—	—	—	—	—	—	—	—	—	12	52
	—	—	—	—	—	—	—	—	—	—	(48.0)	(4.3)
M. macrodactylus	—	—	—	—	6	76	—	—	—	—	—	—
	—	—	—	—	(13.6)	(12.7)	—	—	—	—	—	—
macronyssid, n. sp.	—	—	14	29	12	212	—	—	—	—	1	1
	—	—	(18.0)	(2.1)	(27.2)	(17.7)	—	—	—	—	(4.0)	(1.0)
Steatonyssus antrozoi	6	93	—	—	—	—	—	—	—	—	—	—
	(28.6)	(15.6)	—	—	—	—	—	—	—	—	—	—
S. emarginatus	—	—	—	—	—	—	—	—	1	5	—	—
	—	—	—	—	—	—	—	—	(3.0)	(5.0)	—	—
S. furmani	—	—	—	—	—	—	1	4	—	—	—	—
	—	—	—	—	—	—	(20.0)	(4.0)	—	—	—	—

TABLE 2—(Continued)

S. occidentalis	—	—	39	404	—	—	—	—	—	—	—	—
	—	—	(50.0)	(10.4)	—	—	—	—	—	—	—	—
Spinturnicidae												
Spinturnix americanus	1	1	1	3	—	—	—	—	—	—	—	—
	(4.8)	(1.0)	(1.3)	(3.0)	—	—	—	—	—	—	—	—
S. bakeri	—	—	22	39	—	—	—	—	—	—	—	—
	—	—	(28.2)	(1.8)	—	—	—	—	—	—	—	—
S. orri	4	24	—	—	—	—	—	—	—	—	—	—
	(19.0)	(6.0)	—	—	—	—	—	—	—	—	—	—
Trombiculidae												
Albeckia senase	—	—	—	—	—	—	—	—	2	6	—	—
	—	—	—	—	—	—	—	—	(6.1)	(3.0)	—	—
Leptotrombidium myotis	3	111	4	22	4	58	—	—	1	1	—	—
	(14.3)	(37.0)	(5.1)	(5.5)	(9.1)	(14.5)	—	—	(3.0)	(1.0)	—	—
Loomisia univari	—	—	—	—	—	—	—	—	3	7	—	—
	—	—	—	—	—	—	—	—	(11.0)	(2.0)	—	—
Whartonia perplexa	3	7	—	—	—	—	—	—	—	—	—	—
	(14.3)	(2.2)	—	—	—	—	—	—	—	—	—	—
Myobiidae												
Acanthophthirius caudatus eptesicus	—	—	2	3	—	—	—	—	—	—	—	—
	—	—	(2.6)	(1.5)	—	—	—	—	—	—	—	—
A. oregonensis	—	—	—	—	—	—	—	—	2	2	—	—
	—	—	—	—	—	—	—	—	(6.0)	(1.0)	—	—
Pteracarus aculeus	—	—	2	2	—	—	—	—	—	—	—	—
	—	—	(2.6)	(1.0)	—	—	—	—	—	—	—	—
Notoedridae												
Notoedres (Bakeracarus) sp.	—	—	2	5	—	—	—	—	—	—	2	3
	—	—	(2.6)	(2.5)	—	—	—	—	—	—	(8.0)	(1.5)

*Percent hosts infested and average number of mites per infested host indicated in parentheses.

were the two species commonly found on *Myotis* spp., *Marcronyssus crosbyi* and *Spinturnix americanus*, and the new macronyssid. Five specimens of *Notoedres* (*Bakeracarus*) sp. were found, along with one each of *Cryptonyssus desultorius, Spinturnix bakeri, S. globosus, Pteracarus* sp. closely resembling *P. minutus daubentoni* (pers. comm., A. Fain), *Acanthophthirius* sp. near *gracilis, Leptotrombidium myotis*, and *Alabidocarpus calcaratus.*

Spinturnix globosus was previously known from the anus of *Myotis sodalis* and *M. grisescens* in the eastern United States (Rudnick 1960). *Acanthophthirius gracilis* was described from *Myotis keenii* from Indiana (Fain and Whitaker 1976), and *Leptotrombidium myotis* was found on several species of Oregon bats in this study. *Pteracarus minutus daubentoni* was described from *Myotis daubentoni* and *M. myotis* in Czechoslovakia (Dusbabek 1973). Mites previously reported from *Myotis volans* are *Macronyssus crosbyi, Pteracarus chalinolobus, Spinturnix americanus*, and *Leptotrombidium myotis* (Whitaker and Wilson 1974, Andersen and Jones 1971).

New distributional records: *Cryptonyssus desultorius*, 1 protonymph, Jackson Co., Mt. Ashland, E. Pilot Rock Spring, 28 August 1974. *Spinturnix bakeri*, 1 ♀, Wallowa Co., 11.5 mi NNE Wallowa, Rockwall Spring, 13 August 1975. *S. globosus*, 1 ♀, Jackson Co., Mt. Ashland, E. Pilot Rock Spring, 28 August 1974. *Pteracarus* sp. nr. *minutus daubentoni*, 1 ♀, same date. *Acanthophthirius* sp. nr. *gracilis*, 1 ♀, Malheur Co., Pole Creek, 29 June 1975. *Alabidocarpus calcaratus*, 3 ♀, 11.5 mi NNE Wallowa, Rockwall Spring, 11 August 1977. *Notoedres* (*Bakeracarus*) sp., 4 ♀, 1 protonymph, Jackson Co., Mt. Ashland, E. Pilot Rock Spring, 28 August 1974. All of the above records are new for *Myotis volans* and for the state of Oregon.

Small-footed myotis **(Myotis leibi)**

One individual of this relatively rare bat was examined. It harbored four individuals of *Leptotrombidium myotis.* This chigger, as well as *Spinturnix americanus* and *Macronyssus crosbyi*, have previously been reported from this host (Turner 1974, Whitaker and Wilson 1974).

Little brown myotis **(Myotis lucifugus)**

Fifty-two of 154 bats (33.8 percent of this species were parasitized. The two most abundant parasites were usual ones for this host, *Macronyssus crosbyi* and *Spinturnix americanus* (Radovsky 1967, Rudnick 1960). Other abundant forms were the new macronyssid species and *Leptotrombidium myotis.*

Numerous species of mites have been recorded from the little brown myotis (Whitaker and Wilson 1974, Yunker 1958).

New host record: *Cryptonyssus desultorius*, 2 protonymphs, Hood River Co., Vienti Park, 6.5 mi. W. Hood River, 3 August 1974; L. Keller, coll.

Yuma myotis **(Myotis yumanensis)**

Twenty-one of 46 Yuma myotis (45.7 percent) were found to have mites. The three species most often associated with *Myotis* spp. in Oregon were found: *Spinturnix americanus, Macronyssus crosbyi*, and the new macronyssid species. Mites previously reported from this host are *Alabidocarpus calcaratus, Macronyssus crosbyi, Steatonyssus emarginatus*, and *Spinturnix americanus* (Whitaker and Wilson 1974).

Pallid bat (**Antrozous pallidus**)

Parasites found on 8 of 21 pallid bats (38.1 percent) included two chiggers, *Leptotrombidium myotis* and *Whartonia perplexa*, a macronyssid, *Steatonyssus antrozoi*, and two spinturnicids, *Spinturnix americanus* and *S. orri*. All of these species were previously found on this host in various western states (Brennan and Beck 1956, Vercammen-Grandjean and Langston 1976, Whitaker and Easterla 1975). A single specimen of a listrophorid mite, *Listrophorous mexicanus*, was taken on one pallid bat of this study. We consider this record to represent an accidental association, inasmuch as *L. mexicanus* is a parasite specific for microtine rodents.

New Oregon records: *Steatonyssus antrozoi*, 3 ♀, 4 ♂, 16 protonymphs on 2 hosts, Harney Co., 3.3 mi. S. Princeton, 13 July 1975; 3 ♀, 1 ♂, 7 protonymphs, Union Co., Meadow Creek, 21 June 1976; 1 ♂, 51 protonymphs from 3 hosts, Malheur Co., Dry Creek, 30 July 1976.

Big brown bat (**Eptesicus fuscus**)

Parasites were found on 49 of 78 bats (62.8 percent) of this species. Most abundant were *Steatonyssus occidentalis* and *Spinturnix bakeri*, both common parasites of this bat. Other species frequently found were the new macronyssid species reported above, and the chigger, *Leptotrombidium myotis*. The latter has previously been reported from this host (Yunker 1958). Also found were *Cryptonyssus desultorius, Macronyssus crosbyi, Spinturnix americanus, Acanthophthirius caudatus eptesicus, Pteracarus aculeus, Notoedres* (*Bakeracarus*) sp., and a single specimen of a common rodent parasite, *Androlaelaps fahrenholzi*, which was obviously a contaminant. *Macronyssus crosbyi* and *Spinturnix americanus* are typically parasites of *Myotis* spp. but have occasionally been recorded from *Eptesicus fuscus* (Whitaker and Wilson 1974). *Acanthophthirius caudatus eptesicus* was recently described from *Eptesicus fuscus* in Indiana (Fain and Whitaker 1976); this is the first report of its occurrence outside of that state. *Pteracarus aculeus* was described from *Eptesicus melanopterus* in Surinam and from *E. fuscus* in California (Dusbabek 1973). To our knowledge, *Notoedres* (*Bakeracarus*) sp. has not previously been reported from *Eptesicus fuscus*.

New distributional records: *Spinturnix bakeri*, 1♂, Benton Co., 11 mi S Corvallis, 1 May 1970; 2 ♂, Benton Co., Wm. L. Findley, National Wildlife Refuge, 3 June 1974; 1 ♀, 1 ♂, Malheur Co., Pole Creek, 29 June 1975; 10 ♀, 2 ♂ from 6 hosts, Harney Co., Catlow Valley, 12 July 1975; 6 ♀, 1 ♂, 1 protonymph from 3 hosts, Harney Co., Malheur National Wildlife Refuge, 14 July 1975; 1 ♀, Harney Co., Steens Mtns., 1 mi SE Blitzen Crossing Campground, 4 August 1975; 2 ♀, Union Co., Starkey Experimental Forest, Meadow Creek, 11 July 1976; 1 ♂, Wallowa Co., Powwatka Ridge, 12 August 1977; 4 ♀, 3 ♂ from 4 hosts, Baker Co., 8 mi NE Unity. *Acanthophthirius caudatus eptesicus*, 1 ♂, Harvey Co., Malheur National Wildlife Refuge, 14 July 1975. *Pteracarus aculeus*, 1 ♂, Josephine Co., Jumpoff Joe Creek, 29 August 1974. *Notoedres* (*Bakeracarus*) sp., 3 ♂, Deschutes Co., Indian Ford Campground, 22 August 1974; 2 ♂, Josephine Co., Jumpoff Joe Creek, 29 August 1974.

Of the above species, the first three are new for Oregon, and the last is new for *Eptesicus fuscus*.

Silver-haired bat (**Lasionycteris noctivagans**)

Twenty-one of 44 bats of this species (47.7 percent) yielded three species of mites.

Most abundant were the new macronyssid and *Macronyssus macrodactylus*. The third form recovered was the chigger, *Leptotrombidium myotis*. The last two species have previously been reported from the silver-haired bat (Turner 1974, Whitaker and Wilson 1974). Turner (1974) also recorded *Macronyssus unidens* from *L. noctivagans*, but this mite was not seen in the present study.

New Oregon records: *Macronyssus macrodactylus*, 22 ♂, 3 ♀, 1 pn, Lincoln Co., Cascade Head Experimental Forest, 8 August 1972; 8 ♂, 1 ♀, 1 protonymph, Deschutes Co., Indian Ford Campground, 22 August 1974; 2 protonymphs, Malheur Co., Cottonwood Creek, 10 September 1976; 2 ♂, 1 ♀, 1 protonymph, Wallowa Co., Powwataka Ridge, 12 August 1977; 3 ♂, 3 ♀, Grant Co., T11S, R30E, 28 July; 1 ♀, 1 protonymph, same data but 4 September 1977.

Hoary bat (**Lasiurus cinereus**)

Only one of five bats examined (20 percent) had ectoparasites, *Steatonyssus furmani*. This species, as well as *Chiroptonyssus robustipes* and *Pteracarus chalinolobus*, has previously been reported from *Lasiurus cinereus* (Whitaker and Wilson 1974).

New Oregon record: *Steatonyssus furmani*, 4 ♀, Baker Co., 8 mi NE Unity, 11 July 1977.

Western pipistrelle (**Pipistrellus hesperus**)

Although only five of 33 western pipistrelles (15.2 percent) had mites, five species were found. The usual macronyssid of pipistrelles, *Steatonyssus emarginatus*, was taken along with three chiggers, *Albeckia senase, Leptotrombidium myotis*, and *Loomisia univari*, and a myobiid, *Acanthophthirius oregonensis*. The other form found, possibly a contaminant, was *Dermacarus* sp., which is not generally a parasite of bats. Both *Loomisia univari* and *Acanthophthirius oregonensis* were described from *P. hesperus* (Brennan 1965, Fain and Whitaker 1978). Of the remaining four species, only *S. emarginatus* had previously been taken from this host (Whitaker and Wilson 1974). Other species known from the western pipistrelle in North America are *Chirophonyssus haematophagus, Cryptonyssus desultorius* and *Whartonia perplexa* (Whitaker and Wilson 1974, Gould 1956). A single record of the bird parasite, *Dermanyssus americanus* from *P. hesperus* is considered accidental (Moss *et al.* 1970).

New distributional records: *Steatonyssus emarginatus*, 4♀, Malheur Co., Succor Creek State Park, 16 June 1974. *Albeckia senase*, 2 larvae, Malheur Co., Owyhee Canyon, 12 May 1975; 4 larvae, same data but 14 May 1975. *Leptotrombidium myotis*, 1 larva, same data but 21 August 1974. *Loomisia univari*, 1 larva, same data. Prior to this study none of the above species had been reported from Oregon. In addition, two of the trombiculid species, *A. senase* and *L. myotis*, are first records for *Pipistrellus hesperus*.

Western big-eared bat (**Plecotus townsendi**)

Twelve of 21 bats of this species (57.1 percent) had parasites. The only common mite of this host was *Macronyssus longisetosus*, which was found on 12 of the individuals. *Notoedres* (*Bakeracarus*) sp. was found on two of the bats. One specimen of *Laelaps kochi*, a parasite of microtine rodents, was also taken, but its presence on *P. townsendi* is undoubtedly accidental. Other mites reported from this host in North America are *Macronyssus crosbyi, M. longisetosus, M. unidens, Steatonyssus antrozoi, Pteracarus chalinolobus, Leptotrombidium myotis*, and *Eubrachylaelaps debilis* (Whitaker and

Wilson 1974, Turner 1974). The occurrence on bats of *Eubrachylaelaps debilis*, a strict rodent parasite, probably represents contamination. Specimens of *Notoedres* (*Bakeracarus*) sp. taken during this study were too damaged for specific determination. However, *N.* (*Bakeracarus*) *lasionycteris corynorhini* was described from *Corynorhinus rafinesquii* (= *Plecotus townsendi*) in West Viringia (Fain 1961).

New Oregon record: *Macronyssus longisetosus*, 1 ♂, Malheur Co., Jordan Crater, 17 July 1974; 32 ♂, 7 ♀, 11 protonymphs on 10 hosts, Jackson Co., Little Butte Creek, 30 August 1974; 1 protonymph, Linn Co., 1½ mi N Big Lake, 4 September 1974.

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Representative specimens were verified as follows: Trombiculidae by Richard B. Loomis (Department of Biology, California State University, Long Beach, California) or W. J. Wrenn (Department of Biology, University of North Dakota, Grand Forks, North Dakota) Notoedridae, Myobiidae and Labidocarpidae by Alex Fain (Institut de Medecine tropicale Prince Leopold, Antwerpen, Belgium). Dr. Loomis also reviewed the manuscript and offered helpful advice.

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Food of Vagrant Shrews (Sorex vagrans) from Grant County, Oregon, as Related to Livestock Grazing Pressures

Abstract

Major foods of the vagrant shrew (*Sorex vagrans*) in a relatively non-grazed portion of a mountain meadow in Grant County were earthworms, spiders, crickets, caterpillars, moths, slugs and snails, and June beetles and their larvae. In two similar areas subjected to greater recent grazing, flightless forms (except caterpillars) were much less used; they were replaced primarily by caterpillars and flying insects. The hypothesized cause for these changes was that grazing trampled and compressed the ground, thus decreasing the populations of some forms.

Introduction

Range management strategies are most often designed and implemented specifically for the purpose of increasing the output of a harvestable crop (forage or animal unit months, AUMs). Foraging or grazing by domestic cattle has direct effects on the vegetation and soil and indirect effects on wildlife of different habitat and trophic levels (Ames 1977). This study, part of a larger project dealing with the effects of forest and range management practices on selected insectivorous wildlife, attempts to describe the differences in food habits of vagrant shrews (*Sorex vagrans*) under different range (mountain meadow) management regimes.

Vagrant shrews were trapped at three closely situated mountain meadow sites in the Blue Mountains, Grant County, Oregon. The three sites, although occurring along only a 1.6 km segment of stream, had different recent management histories and thus provided conditions for comparing the effects of grazing on invertebrate fauna as reflected by shrew feeding habits.

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Methods and Study Sites

The study area, 26.5 km SE of the town of Long Creek, was in the *Abies grandis* zone (Franklin and Dyrness 1973) of the Blue Mountains. Three study sites were situated in the riparian zone along Camp Creek near Eagle Rock (T11S, R32E, S34 and 35).

The specific sites, upstream to downstream, and the respective recent grazing histories were:

1. Upper "fish" pasture (UFP), approximately 8 ha, was fenced in 1963, planted with willow cuttings along the stream, and rested for 2 years. Beginning in 1965, light late-season (after 15 August) cattle stocking was permitted. About 1970, this was changed to light late-season horse use on an intermittent basis.
2. Lower "fish" pasture (LFP), approximately 7.5 ha, was fenced in 1964 and rested for 3 years. Beginning in 1968, moderate late-season (after 1 August) cattle grazing was permitted on an annual basis. Here the objective was to remove about 20 AUMS of forage (1 Ac./AUM) each season.
3. Eagle Meadow (EM). The riparian habitat along Camp Creek, beginning at Eagle Rock and proceeding down Camp Creek, north and west for 3.2 km, was isolated by wire and pole fence in 1975 and protected from cattle grazing. Before that year, the meadow bottom had been grazed season long under a heavy level of stocking. In the spring of 1975, 3000 shrub cuttings were planted along Camp Creek from the north of Eagle Rock Creek on down Camp Creek for about 3.2 km.

Shrews were captured in pitfall traps set in the meadow adjacent to the stream in July and August 1978. The traps consisted of empty five-pound plastic food containers buried in grassland runways, openings flush with the ground, and filled with sufficient water to drown the captured animals. The water prevented escape and cannibalism and increased the chances of obtaining animals with full stomachs. The shrews were collected daily, frozen, and later aged, sexed, and dissected to remove the individual stomachs. Stomachs were preserved in 10 percent formalin for food analysis. Attempts were made to obtain approximately equal sample sizes from the three study sites. Stomach contents were identified, and the percent volume and frequency of each food item in each stomach were visually estimated with a zoom dissecting microscope.

Results and Discussion

Results of stomach analyses are shown in Table 1.

In the Eagle Meadow area, earthworms were the major food, forming 29.4 percent of the volume of food in the sample, whereas in the upper and lower "fish" pastures, earthworms formed only 6.6 and 5.3 percent, respectively.

The most important item in stomachs from the UFP, forming 35.0 percent of the volume, and one of the two most important items (28.0 percent volume) in the LFP was caterpillars. Another food, abundant in these areas, was a white, fatty, amorphous material; it was the top item in the LFP but unfortunately could not be identified.

The second and third most abundant items in EM were spiders and crickets, both being non-flying forms. Spiders were not found in stomachs in either of the fish pasture areas; crickets were found at a lower rate in the upper fish pasture area than in Eagle Meadow, and they were not found at all in stomachs from the lower fish pasture.

TABLE 1. Food from stomachs of shrews, **Sorex vagrans**, from Grant County, Oregon, including 31 from an area with no grazing, 28 from an area lightly grazed (by cows only at the end of each summer), and 32 from an area heavily grazed (by horses for several years, all year).

	No grazing		Light grazing		Heavy grazing	
N =	31		28		32	
	Percent		Percent		Percent	
	Volume	Frequency	Volume	Frequency	Volume	Frequency
Earthworms	29.4	32.3	6.6	10.7	5.3	6.3
Spider	14.5	22.6			3.3	6.3
Cricket	6.5	6.5	3.6	3.6		
Unidentified white material	6.5	6.5	9.3	10.7	29.4	46.9
Caterpillars	6.3	9.7	35.0	39.3	28.0	56.3
Moths	6.0	6.5	12.9	17.9	6.1	6.3
Slug and snail	5.2	6.5				
Unidentified insect	5.0	16.1	3.2	14.3	1.1	3.1
June beetle grubs	4.2	6.5				
Insect larvae	3.2	3.2	5.4	10.7		
Ladybird beetles	2.9	3.2				
Insect eggs	2.4	3.2				
June beetles	2.1	3.2				
Beetle larvae	1.8	3.2	12.1	17.9	3.4	9.4
Centipedes	0.8	3.2	3.0	10.7	1.9	6.3
Ants	0.8	6.5	0.4	3.6	1.6	6.3
Unidentified beetles	0.5	3.2	1.3	7.1	1.6	12.5
Flower parts	0.5	3.2				
Other vegetation	0.5	6.5	0.5	7.1	0.3	3.1
Cranefly	0.5	3.2				
Unidentified flies	0.3	3.2	2.7	10.7	9.0	15.6
Grass seeds	0.3	3.2	0.5	3.6		
Endogone (fungus)	—	—	3.2	3.6	2.8	3.1
Harvestmen	—	—	0.4	3.6		
Aphids	—	—	—	—	2.8	6.3
Moth cocoons	—	—	—	—	2.0	3.1
Hemipteran (bugs)	—	—	—	—	1.1	3.1
Grasshoppers	—	—	—	—	0.3	3.1
Unidentified bees and wasps	—	—	—	—	0.2	3.1
	100.2		100.1		100.2	

Other flightless forms found in stomachs in EM, but lacking in the other areas, were slugs and snails and June beetle grubs. Adult June beetles fly, but they were lacking in the other areas—apparently because of the lack of larvae. Thus, non-flying items living on or in the soil serve as food in the EM site but are less important or are not found in stomachs in the other areas.

The major types of foods eaten by shrews in the recently grazed UFP and LFP areas are flying insects. Total insects eaten by shrews in the recently non-grazed EM site (excluding crickets and June beetles and their larvae) formed 29.7 percent of the volume. On the UFP and LFP sites comparable figures were 73.0 percent and 57.2 percent.

We have no direct data on relative availability of foods between the three study sites. Terry (1978) suggested that *Sorex vagrans*, as well as other sympatric Insectivora in western Washington, are generalists with respect to food; she further suggested that it is selectively advantageous for them to eat anything that is available which provides sufficient nutrition or energy. Availability has both intrinsic and extrinsic components. Intrinsic components include the various adaptations (morphological, physiological, behavioral) that allow an individual or species to obtain and process food. Included are those specialized characteristics that reduce competition through resource partitioning.

Extrinsically, availability is determined by such things as abundance (both absolute and relative), cover, and activity of food items. All of these, in turn, may be influenced by both biological and physical environmental factors. Food preference, which may be influenced by palatability and ease of attainment of the various possibilities, is very important when food supplies are more than adequate. With diminishing supplies, food eaten probably more closely approaches the proportions actually present. Assuming that *S. vagrans* is more of a generalist than a specialist, its diet should reflect differences in abundance and/or attainability of food. Both of these factors are extrinsic components of availability with potential for impact from environmental change.

Although the three study sites were in close proximity and the macrohabitats similar, the shrew food habits were different at each of the sites. Table 2 shows two quantitative comparisons that illustrate these differences. To compare similarity of food species composition among areas, a coefficient of community (quotient of similarity, Sorenson 1948) was calculated for all possible pairwise combinations of grazing sites: $\frac{2C}{A+B}$, where C = no. of species common to both sites and A or B = no. of species at a site. All the areas are moderately similar (where 1.0 = complete similarity), with EM and LFP the least similar to one another. To compare the relative amounts of various food items in the diets of shrews from the three study sites, they were ranked according to decreasing percent volume and a Spearman rank correlation coefficient (Zar 1974) calculated for the possible pairwise combinations of grazing sites. Again, all sites have a relatively low correlation coefficient, and EM and LFP showed the lowest correlation, if all food items are considered, or next to lowest if just the top 10 food items are considered. In either case, the EM site shows the lowest correlation with the other two, and the UFP and LFP show the highest correlation with each other.

TABLE 2. Pairwise quantitative comparison of the similarity measured by coefficient of community (CC) and ranking measured by Spearman rank correlation (SRC) of food items taken at the three study sites.

		Sites compared		
		EM and UFP	UFP and LPF	EM and LFP
CC		.737	.705	.600
SRC	(all)	.324	.410	.207
	(top 10)	.173	.422	.238

These data indicate that differing grazing regimes have resulted in changes in the invertebrate fauna, as reflected by shrew feeding habits. One plausible explanation for the cause of the differences is that the trampling of the ground by livestock compressed the soil to the point that the organisms normally living in or on it were less abundant. Replacing them as shrew foods in the more heavily grazed areas were caterpillars, moths, and a number of flying insects. Soil compaction readings support this view. Fifty measurements randomly distributed around the shrew trap sites within 1.0 m of the creek were taken in August 1979 in each of the three study areas with a Soil Test pocket pentrometer. A spring calibrated from 0 to 4.5 units was compressed, while a blunt rod, 6.0 mm in diameter, was gradually pushed into the soil. The index value measured in kg/cm^2 (tons/ft^2) was in direct proportion to the soil strength. The results showed the Eagle Meadow site to be the least compacted ($x = 2.00$ kg/cm^2,

$S = 1.15$), whereas the upper fish pasture ($\bar{X} = 2.18$ kg/cm^2, $S = .96$) and lower fish pasture ($\bar{X} = 2.50$ kg/cm^2, $S = .97$) had higher readings, possibly the result of higher grazing pressure. Further support came from the higher soil strength readings ($\bar{X} = 2.61$ kg/cm^2, $S = 1.08$) obtained from the heavily grazed stock watering corridor between UFP and LFP.

In summary, the site with the least amount of recent grazing pressure (EM) had the least compacted soil and the greatest amount of soil-dwelling organisms, such as eathworms, in the shrew diets. Additionally, this site showed the least similarity of food items and least correlation of ranked food items as compared to the other two sites.

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Mid-Columbia River Zooplankton

Abstract

Zooplankton samples were collected from the Columbia River at the Hanford Site, Washington, from June 1973 through March 1980. Samples were collected at river kilometer (Rkm) 611 and Rkm 566. Crustacean-zooplankton numerically dominated most samples. *Bosmina, Diaptomus,* and *Cyclops* were the dominant genera observed. Zooplankton densities generally followed a trend of winter minimums and late-spring, early-summer maximums.

Introduction

Zooplankton samples were collected from the Columbia River at Hanford (Fig. 1) from June 1973 through March 1980. Samples were collected at river kilometer (Rkm) 611 from June 1973 through June 1974 and at Rkm 566 from December 1974 through March 1980 for the Washington Public Power Supply System's Columbia River aquatic ecological studies (Page *et al.* 1976; Gray *et al.* 1976; Gray and Page 1977, 1978, 1979a, 1979b; Beak 1980). Study objectives included identification of Columbia River zooplankton at Hanford and determination of their relative abundance and seasonal distribution.

Methods

River Kilometer 611

Weekly zooplankton samples were taken between June 1973 and June 1974 from depths at three stations across the river. Five samples were taken on the night following a day sample. Samples were collected with a Clarke-Bumpus plankton sampler equipped with a Number 10 (158μ) plankton net. Because of a strong current in the Columbia River, it was possible to operate (in effect, tow) a Clark-Bumpus sampler from the stern of an anchored boat. Often, however, it was necessary to drift downstream to avoid sampling velocities beyond the capability of the sampler. Bottom samples were taken within 1 m of the bottom, and mid-depth samples were taken about halfway between the surface and the bottom. Surface samples were taken with the sampler just below the water surface. The sampler was towed for 3 to 5 min. Material collected was washed into a sample jar and preserved in 4 percent formalin. Aliquots from the sample jar were microscopically examined in the laboratory to determine the number and species of organisms present.

River Kilometer 566

A 153μ mesh net with a 30-cm diameter mouth and a 5:1 length to diameter ratio

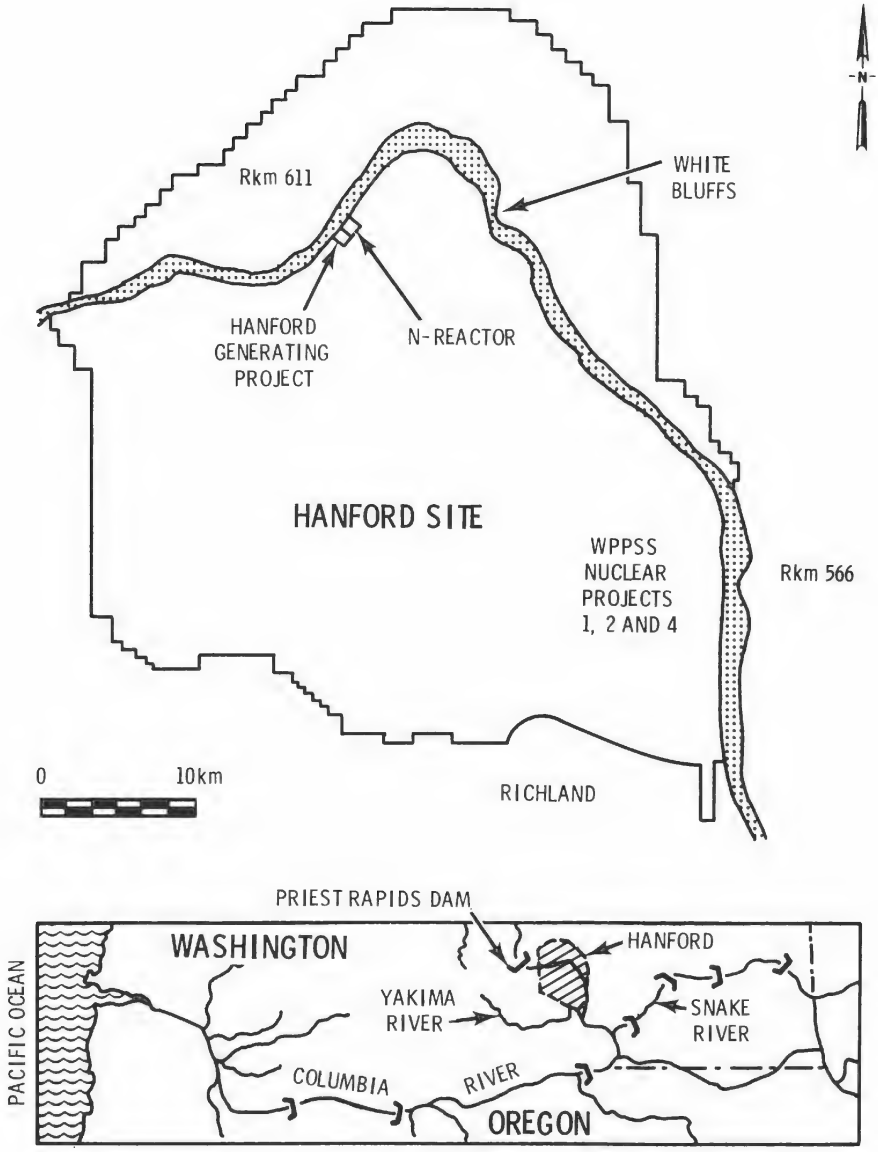

Figure 1. Map of the Hanford Site, southeastern Washington.

was used to collect samples at Rkm 566. Samples were taken once in 1974, six times in 1975, quarterly in 1976, and once each month from 1977 through March 1980. Duplicate stepped-oblique zooplankton tows were taken. This sampling method integrated the sample over depth. Vertical stratification of zooplankton was not examined in this study because samples, taken weekly for a year at Rkm 611, indicated mid-Columbia River zooplankton are not vertically stratified. The net was towed for a total of 3 min by holding it at the surface for ½ min, lowering to mid-depth for ½ min, lowering to the bottom for 1 min, raising to mid depth for ½ min and finally raising to the surface for ½ min. This usually resulted in filtering of 5 to 5.5 m^3 of water. The net was retrieved and the sample was washed into a jar and preserved in 4 percent formalin.

Results

Taxa (Rkm 611)

The crustacean-zoolplankton community at Rkm 611 during 1973 and 1974 consisted of 12 species (Table 1). Ten cladocerans, one calanoid, and one cylopoid copepod were identified. *Bosmina longirostrus* was the most abundant cladoceran and the dominant zooplankter from June until October, when *Diaptomus ashlandi* became dominant. This species remained dominant until June 1974. Prior to January 1974, *Cyclops bicuspidatus thomasi* was the third most abundant organism. During the January-February thaw, *C. bicuspidatus thomasi* became the second most abundant zooplankter and remained so until it became dominant in June 1974. *Daphnia* spp. were the fourth most abundant organisms, but they were present in such low numbers that, for the most part, they accounted for only 10 percent of the animals present. *Bosmina, Diaptomus*, and *Cyclops* accounted for most of the remaining 90 percent (Fig. 2).

Other types of invertebrates were observed in the samples. These included insect larvae, aquatic arachnids, annelids, rotifers, nematods, Tardigrades, and Hydras. Drifting insect larvae, especially trichopterans and dipterans, were present in limited numbers.

Insect larvae usually accounted for less than 5 percent of the animals collected. In mid-October, relative abundance of insect larvae peaked at 5 percent of the community. Numbers of insect larvae peaked with other zooplankton in mid-July at about 7 larvae/m^3. This peak corresponded with peak insect larvae numbers observed in the benthos collections. However, relative abundance was low, and at this time insect larvae represented only about 0.08 percent of all zooplankton. These data indicate that drifting insects are not numerically important components of the zooplankton community at Rkm 611.

Taxa (Rkm 566)

Fifty-eight zooplankton taxa were observed in samples collected at Rkm 566 from December 1974 through March 1980 (Table 1). Seasonal relative abundance was dominated by three crustacean genera: *Bosmina, Diaptomus*, and *Cyclops* (Fig. 2). *Bosmina* generally dominated the July, August, and September samples. *Diaptomus* dominated December and January samples. *Cyclops* dominated March and June samples. In the late-winter, early-spring of 1977, rotifers dominated the samples. Insect larvae were only numerically significant in samples collected in March 1975 and September 1976.

TABLE 1. Zooplankton taxa collected in samples from the Columbia River at river kilometer 611 and 566 from June 1973 through March 1980. (1 = Rkm 611, 2 = Rkm 566, 3 = observed at both sites.)

Coelenterata	
Hydra spp.	(3)
Bryozoa	
Ectoprocta	
Paludicellidae	
Paludicella articulata	(2)
Annelida	
Oligochaeta	(3)
Hirudinea	(3)
Aschelminthes	
Nematoda	(2)
Rotifera	
Brachionidae	
Kellicottia longispina	(2)
K. spp.	(2)
Keratella cochlearis	(2)
K. quadrata	(2)
Brachionus spp.	(2)
Euchlanis spp.	(2)
Lecanidae	
Lecane spp.	(2)
Synchaetidae	
Synchaeta spp.	(2)
Polyarthra sp.	(2)
Testudinellidae	
Testudinella spp.	(2)
Arthropoda	
Tardigrada	(3)
Crustacea	
Cladocera	
Leptodoridae	
Leptodora kindtii	(3)
Sididae	
Sida crystallina	(2)
Latona spp.	(2)
Diaphanosoma spp.	(2)
Daphnidae	
Daphnia spp.	(2)
D. pulex	(1)
D. middendorffiana	(1)
Ceriodaphnia spp.	(2)
Bosminidae	
Bosmina longirostris	(3)
Macrothricidae	
Macrothrix spp.	(2)
Ilyocryptus spp.	(2)
Chydoridae	
Pleuroxus spp.	(2)
P. denticulatus	(1)
Alona costata	(1)
A. quadrangalaris	(1)
A. guttata	(1)
A. rectangula	(1)
Chydorus spp.	(2)
Eurycercinae	(2)
Eurycercus lamellatus	(1)
Ostracoda	
Copepoda	
Calanoida	
Temoridae	
Epischura spp.	(2)
Temoridae copepodid	(2)
Diaptomidae	
Diaptomus spp.	(2)
D. ashlandi	(3)
Cyclopoida	
Cyclopidae	
Cyclops spp.	(2)
Bleuspidatus thomasi	(3)
Harpacticoida	(3)
Amphipoda	(3)
Acari	(3)
Insecta	
Collembola	(2)
Ephemeroptera	(2)
Trichoptera	
Rhyacophilidae	(2)
Hydropsychidae	(3)
Diptera	
Chironomidae	(2)
Simuliidae	
Simulium sp.	(2)
Platyhelminthes	
Turbellaria	
Dugesia sp.	(2)
Protozoa	
Vorticella sp.	(2)

Density (Rkm 611)

Numbers of zooplankton ranged from 1500 organisms/m^3 in mid-July to <30 organisms/m^3 in November and December (Fig. 3). The yearly average was 607 organisms/m^3. Numbers of zooplankton declined steadily from a July peak to a November/December low. A minor peak occurred in January and February, which corresponded with an early thaw and upstream flooding and may have represented organisms washed from upstream reservoirs.

Density (Rkm 566)

Zooplankton densities at Rkm 566 generally followed a trend of winter minimums and late-spring, early-summer maximums (Fig. 3). Average numbers of zooplankton per cubic meter (No/m^3) ranged from less than 10 in December 1974 to 4702 in June 1977.

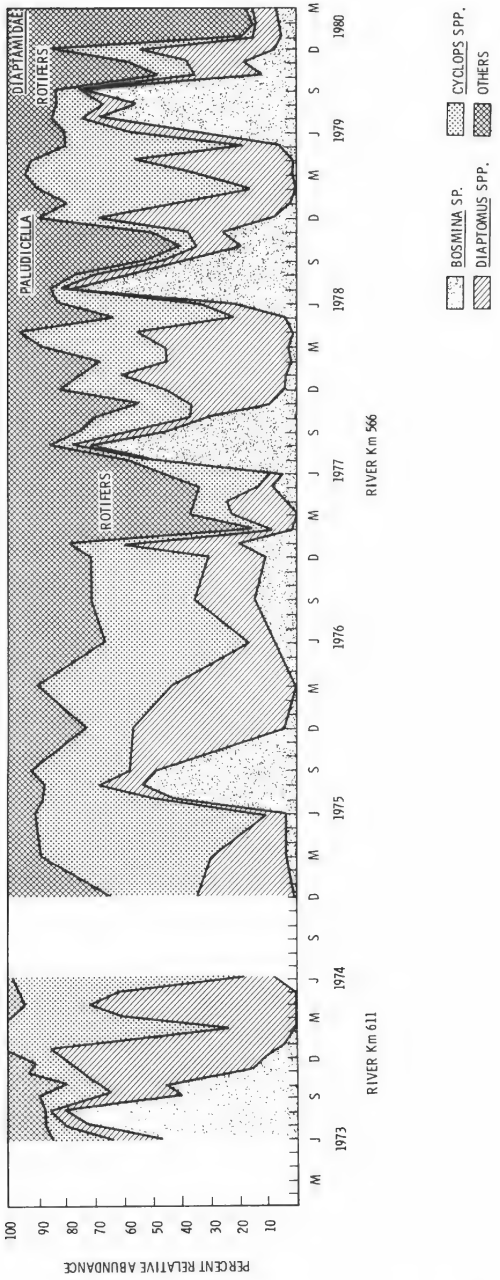

Figure 2. Relative abundance (percent of mean total number) of the three dominant zoolplankton organisms collected at Rkm 611 and Rkm 566, June 1973 to March 1980 (modified from Beak 1980).

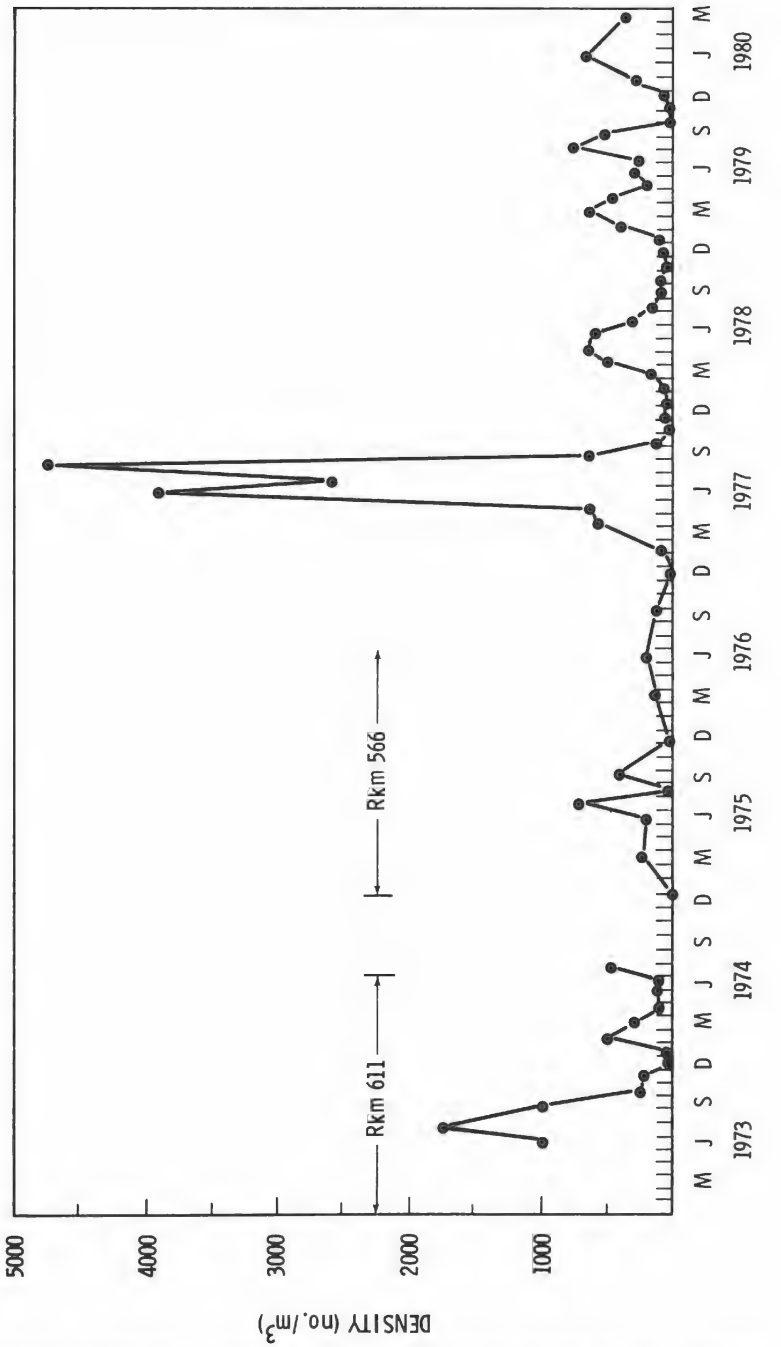

Figure 3. Number of Columbia River zooplankters per m^3 collected at river kilometer 611 and 566.

Summary

Crustacean zooplankters dominated most samples collected at Rkm 611 and Rkm 566 from June 1973 through March 1980. The three dominant genera were *Bosmina, Diaptomus*, and *Cyclops*. Density estimates were lowest in the winter and highest in the summer. Summer peaks were dominated by *Bosmina* and ranged to densities greater than 4500 organisms/m^3. Winter density estimates were generally less than 50 organisms/m^3. *Diaptomus* and *Cyclops* dominated in winter and spring, respectively.

Acknowledgments

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Vertebrate Fossils from the Chuckanut Formation of Northwest Washington

Abstract

A single specimen containing a cast of a turtle carapace and a bone fragment from a larger animal are the first vertebrate fossils found in the Chuckanut Formation. The Clark Point outcrops (Whatcom Co., Wash.) where this specimen was collected also contain large calcareous concretions that superficially resemble bones or logs. These pseudofossils probably account for local tales of a fossil dinosaur reported from the Chuckanut Formation.

Introduction

Excavation of foundation trenches for a house built in 1960 near Bellingham, Whatcom Co., at Clark Point (T 37 N, R 2 E, SW corner Sec 13) uncovered a piece of siltstone that contains the first vertebrate fossils found in the Chuckanut Formation. The property owners, Mr. and Mrs. Douglas Clark, assumed the specimen to be a mollusc shell or leaf imprint, but their loan of the specimen to the Western Washington University Geology Department in the spring of 1981 led to recognition that the rock contains the cast of the interior surface of a turtle carapace and a bone fragment from a larger animal. Though carbonized leaves and log casts are abundant in the Chuckanut Formation, the only previously known animal fossils are fresh-water molluscans found at a few inland localities (Pabst 1966).

Previous Paleontology Studies

The Chuckanut Formation consists of a thick, strongly folded series of arkosic sandstone, shale, and conglomerate beds exposed on the western flanks of the North Cascades in Whatcom, Skagit, and northern Snohomish counties, Washington. Stratigraphic measurements by Glover (1935) and Weaver (1937) indicate a total thickness of about 3000 m along Chuckanut Drive, whereas Miller and Misch (1963) report 4600 m, and possibly 6100 m of section east of American Sumas Mountain near the U.S.-Canada border.

Paleontologic studies began in 1841, when James Dwight Dana of the Wilkes Exploring Expedition collected plant fossils from Bellingham Bay. Descriptions of plant species were published by Lesquereux (1859), Newberry (1863), and Knowlton (1902). Detailed paleobotany studies were made from 1948 to 1952 by Pabst, and a posthumous monograph (1966) contains a review of the paleobotany and paleoecology

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of these rocks. Ill health prevented Pabst from completing studies of the abundant angiosperm fossils, and her published work includes only the ferns, conifers, and rushes. Pabst believed the Chuckanut sediments were deposited in a continental basin having a warm-temperate to subtropical climate, with a flora similar to the lowland rain forests presently found in Mexico, Central America, and northern South America. Palynological investigation of the lower 1555 m of the type section (Griggs 1966) indicates the presence of more than a dozen species of flowering plants and generally confirms Pabst's interpretation of the paleoecology. Sediment characteristics indicate that deposition occurred mostly along meandering rivers and adjacent floodplains (Johnson 1981).

Chuckanut plant fossils are similar to early Tertiary floras from other western localities, particularly the Paleocene Fort Union Formation. Pabst believed the lowermost Chuckanut was very late Cretaceous, with the rocks being predominantly Paleocene. Radiometric dates suggest that the sediments are somewhat younger than previously recognized. Frizzel (1979) refers to the Chuckanut as being early to middle Eocene, based on a single fission track date of 50 my from the upper part of the stratigraphic section. Fission track dates of detrital zircon have recently been obtained at the University of Washington for about a dozen specimens of Chuckanut sediment and confirm that the formation is early to middle Eocene (Samuel Johnson, pers. comm.).

Vertebrate Remains

The turtle fossil (Fig. 1) was excavated from a thinly bedded siltstone layer within a series of beds which are predominately sandstone. The carapace is 12 cm long, 13 cm wide, and 2.5 cm deep, having a nearly circular outline and low arch. The cast represents the bony dermal shell, marked by 9 shallow corrugations on either side of the vertebral column. The specimen is somewhat eroded, but remnants of the original bone are present. X-ray fluorescence analysis shows that this material consists of calcium phosphate, and SEM examination reveals preservation of fibrous organic matrix (Fig. 2). Vertebral processes are preserved as a central line, representing dorsal vertebra 1-10, with faint indications of the first sacral vertebra. Nine pairs of free ribs attach to the vertebral column, fused to the dermal shell 0.5-1.0 cm from the vertebra, with the ribs forming the valleys of the shell corrugations.

The specimen lacks characteristics needed for complete identification, but general features place it in the Testudinoidea superfamily (Roemer 1968). Members of this group are known from late Cretaceous to Recent and include most living pond and swamp turtles. Two carapaces identified as *Baptemys* were reported from the Roslyn Formation (Wheeler 1955), a sedimentary unit from Eastern Washington similar in age and lithology to the Chuckanut. *Baptemys* belongs to the Dermatemydidae family, a primitive testudinoid group from the late Cretaceous and Eocene of North America.

One cm below the carapace the rock contains a fragment of bone too large to have come from the turtle (Fig. 3). The fragment is exposed in cross section and has a flattened assymetric 26 by 6 mm oval shape. A dense 0.5 mm cortical layer encloses the porous inner material. Though too incomplete to be identified, this bone indicates that the Chuckanut depositional basin was inhabited by some larger vertebrate.

Clark Point consists of steeply dipping beds of arkosic sandstone interlayered with lesser thicknesses of sandy shale and conglomerate. These beds are stratigraphically

Figure 1. Cast of the interior surface of turtle carapace from Clark Point, near Bellingham, Washington.

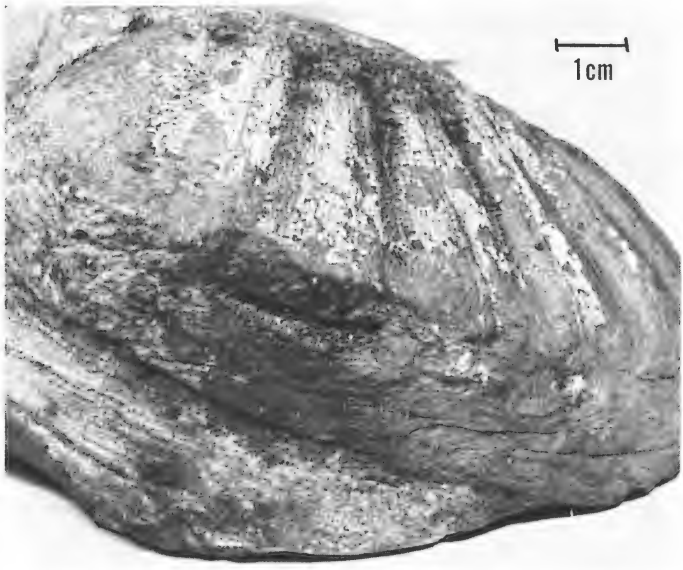

Figure 2. Side view of specimen, showing porous bone fragment, and remnants of original dermal shell.

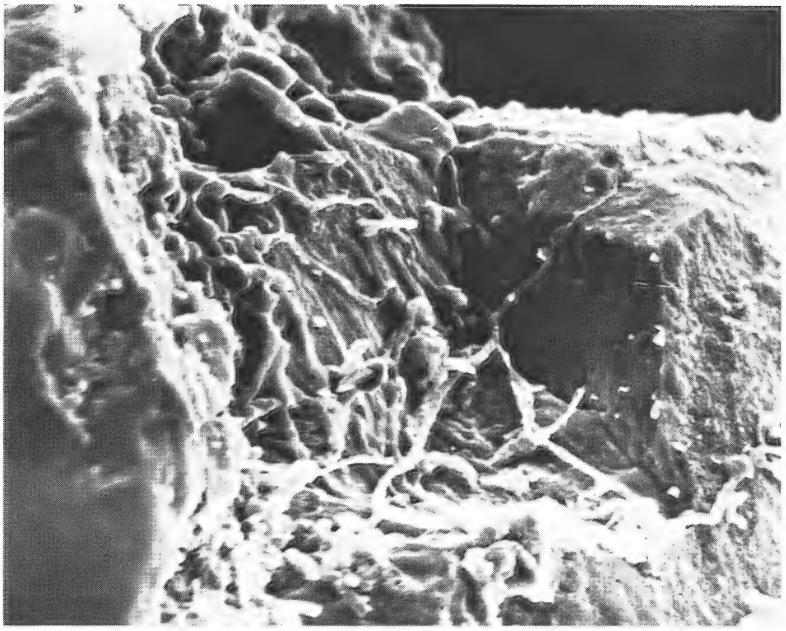

Figure 3. SEM photomicrograph of turtle shell material, showing organic matrix. 345X magnification.

slightly above the Chuckanut Bay outcrop dated at 50 my by Frizzel (1979). The exact site where the turtle fossil was found is no longer accessible, but this stratum is exposed in nearby beach cliffs. Examination of these rocks turned up no additional vertebrate fossils, though carbonized plant material is common.

Pseudofossils

About a dozen large objects resembling fossils are exposed near sea level at a small inlet near the tip of Clark Point. These occur in well-sorted, massively bedded arkosic sandstone and consist of elongate flattened-cylindrical masses typically divided into segments (Fig. 4) that bear a vertebra-like appearance. These objects may account for undocumented reports of fossil reptiles from the Chuckanut Bay area (Hopkins 1966, p. 20; W. H. Mathews, University of British Columbia, pers. comm.). Though superficially resembling vertebra, the objects are too large and lack such details as spinal processes, rib attachments, or articulating surfaces. They are similar in size and shape to casts of logs found throughout the Chuckanut Formation, but lack the carbonized outer layer present at other locations.

The objects are about 10-30 cm in diameter and have exposed lengths of up to 3 m. They are flattened cylinders oriented with the major axial plane parallel to bedding and long axes parallel to each other. These masses are textually identical to the surrounding sandstone but effervesce strongly in dilute HC1, showing that they contain large amounts of calcareous cement. In contrast, like most Chuckanut sediment

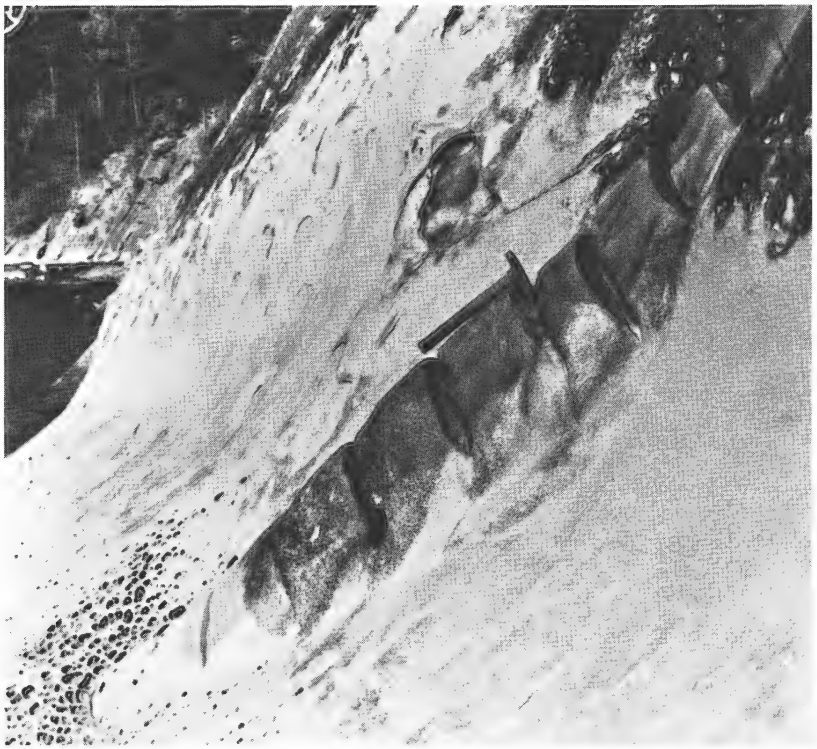

Figure 4. Weathered calcareous concretions exposed on beach cliff at Clark Point.

(Kelly 1970), the surrounding rock is cemented by phyllosilicates. The composition and shape of these objects suggests that they are calcareous concretions.

The segmented appearance results from dissolution of carbonate cement along joint planes that cut the concentrations perpendicular to their long axes. These joints are expressed only in the concretions and do not extend into the adjacent phylosilicate-cemented sandstone. In thin section an estimated 10-20 percent sparry calcite cement can be seen filling pores. Most of the Chuckanut sandstones have phyllosilicate pore fillings and low porosity. The concretions must have formed before the pores were filled with diagenetic phyllosilicates, indicating that their formation was an early event in the history of the rock. The joint fractures may have originated during folding; the fractures do not extend outside the concretions because either the sandstone was not cemented by phyllosilicates when folding took place, or the phyllosilicates behaved more plastically than the carbonate. Calkin (1959) observed "spine-like" calcareous concretions in coastal outcrops of Chuckanut sandstone on Lummi Island. These concretions are abundant but lack the segmented patterns present at Clark Point.

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Fishes of Oxbow Lakes of Washington

Abstract

Fish faunas of oxbow lakes in the Chehalis, Snoqualmie, and Okanogan drainages of Washington were sampled with a minnow seine. For comparison, collections were made in parent streams. We collected fewer fish species from oxbow lakes than from adjacent stream reaches. Most oxbow lake ichthyofaunas were dominated by non-native fishes, while native fishes dominated streams. Numbers of native species and non-native species were not significantly correlated in oxbow lakes ($r = 0.01$), but in Chehalis drainage collections the Olympic mudminnow (*Novumbra hubbsi*) was collected only where we did not collect non-native fishes.

Introduction

Oxbow lakes occur along low gradient, meandering streams. They are formed when a meander is isolated from the parent stream (Reid 1961, Beecher *et al.* 1977). Typically, a number of oxbow lakes occur at irregular intervals along such streams. Different oxbow lakes have been isolated from the parent stream for different lengths of time. Along a parent stream, oxbow lakes vary in age, successional stage, and area or length. Oxbow lake width is approximately equal to parent stream width and does not vary greatly among oxbow lakes along a reach of the parent stream. Consequently, area is proportional to length.

The strictly aquatic fauna of an oxbow lake is derived from the aquatic fauna of the parent stream (Beecher *et al.* 1977). The fauna of the parent stream is a pool of potential colonizers of the oxbow lake when it is formed. The aquatic fauna of the oxbow lake is a selective sample of the aquatic fauna of the parent stream, since isolation of the oxbow lake is a gradual process.

Comparison of a Florida oxbow lake to its parent stream, the Escambia River, showed that the oxbow lake had fewer species of fishes than the parent stream. Reduced habitat diversity was proposed as an explanation for the oxbow lake's lower fish species richness (Beecher *et al.* 1977). In the present study we compared fish species richness in 16 Washington oxbow lakes to that in parent streams.

Magnuson (1976) likened lakes to islands and suggested that they might conform to island biogeography theory. He suggested that introduction of non-native fishes might be expected to cause local extinctions of some other species. If this were true, the number of introduced species should be negatively correlated with the number of

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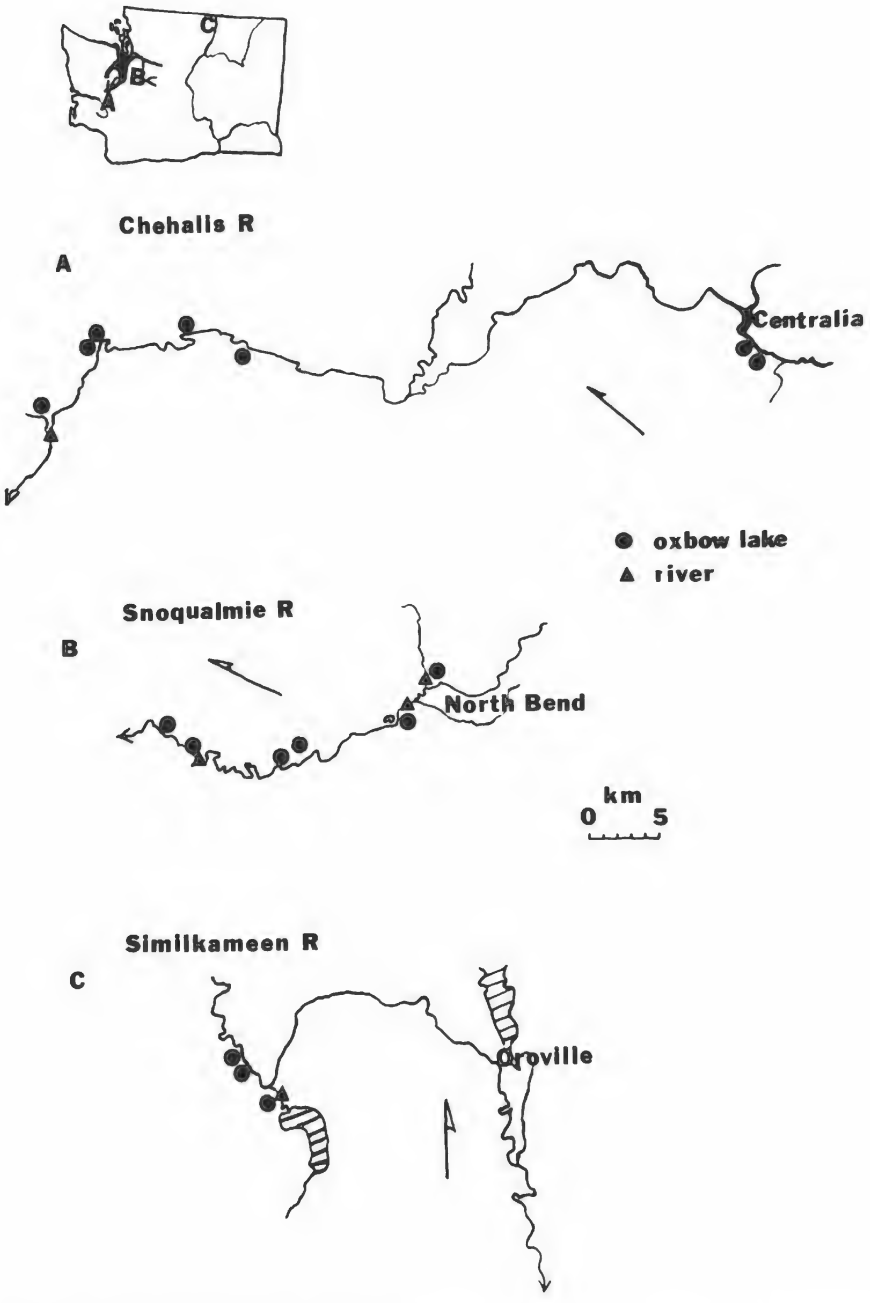

Figure 1. Locations of study sites. Inset shows locations of river systems in the state of Washington.

native species. We examined the relationship between number of native fish species and number of introduced fishes in oxbow lakes.

Methods and Materials

We sampled 16 oxbow lakes and five sites on three parent streams. Study areas were the Chehalis, Snolqualmie (Snohomish), and Similkameen (Okanogan-Columbia) drainages in Washington state (Fig. 1). Using minnow seines of 5.7 x 1.3 m and 4.3 x 1.9 m, with stretch meshes of 5 and 8 mm, respectively, we seined until all accessible habitats were represented in our sampling at each site and until additional seine hauls yielded no additional fish species. We identified, counted, and released salmonids, but other species were preserved in 10 percent formalin for identification and enumeration in the laboratory. Each seine haul was treated as a discrete subsample: the number of species and individuals in individual seine hauls was recorded, with all fish from one seine haul preserved together in a container, but no other specimens went into that container.

Use of small seines reduced our effectiveness in sampling large individuals, but smaller specimens were easily captured. Since most species are represented by more small than large individuals, seine size should not have biased our counts of species greatly. We were unable to sample deep (> 1.5 m) areas effectively.

Results

In all cases we found more fish species in parent streams than in oxbow lakes (Table 1; $t = 4.26$, $df = 19$, $P < 0.01$). The number of fish species in parent stream collections ranged from 6 to 10. The number of fish species in oxbow lakes ranged from 1 to 8. Oxbow lakes with inlet streams generally had more species than did isolated oxbow lakes (Table 2; $t = 2.14$, $df = 14$, $P = 0.05$). The number of species per seine haul followed the same pattern as the number of species per collection, with more species in parent streams than in oxbow lakes (Table 3; $t = 2.02$, $df = 85$, $P < 0.05$).

Among eight species collected only in oxbow lakes, seven were non-native species. The most common non-native fish of oxbow lakes was the largemouth bass (*Micropterus salmoides*), although this was also the only non-native fish we collected in a parent stream; all of the other seven non-native fishes were collected only in oxbow lakes. The prickly sculpin (*Cottus asper*) was the only native fish that we collected only from an oxbow lake. Some oxbow lakes contained only native fishes.

In Washington oxbow lakes, numbers of introduced and native species were not correlated ($r = 0.01$, $n = 16$, $P >> 0.05$). Only native fishes were collected with the Olympic mudminnow (*Novumbra hubbsi*) (Table 4). At each site where we found mudminnows we also collected threespine sticklebacks (*Gasterosteus aculeatus*). The Olympic mudminnow was absent from four Chehalis drainage collections in which non-native fishes were present. The largemouth bass (*Micropterus salmoides*) was either collected, observed, or reported from the four Chehalis basin sites where the Olympic mudminnow was not collected. Segregation of the Oympic mudminnow from non-native fishes appears to be significant ($X^2 = 8.0$, $df = 1$, $P < 0.01$).

In contrast to oxbow lakes, in which non-native fishes were a major component of the ichthyofauna, parent streams were dominated by native fishes. Two salmonids, the mountain whitefish (*Prosopium williamsoni*), and rainbow trout (*Salmo gairdneri*),

TABLE 1. Fishes of oxbow lakes and parent streams. Each column represents a different site. N=non-native fish. +=seen but not collected. *=collected.

Species	Chehalis R. Basin								Snoqualmie R. Basin									Similkameen R. Basin				
	parent stream	oxbow lakes							parent stream	oxbow lakes								parent stream	oxbow lakes			
Petromyzontidae																						
Entosphenus tridentatus	*			*						*												
unid. lamprey ammocoete									*													
Salmonidae																						
Prosopium williamsoni									*	*								*				
Salmo clarki										*				*				*				
S. gairdneri	*								*	*	*											
Oncorhynchus kisutch				*						*					*	*						
Umbridae																						
Novumbra hubbsi	*	*	*			*																
Cyprinidae																						
Cyprinus carpio N							+												*		*	
Richardsonius balteatus	*																	*				
Rhinichthys cataractae	*								*	*	*		*									
R. falcatus																		*				
R. osculus	*																					
Ptychocheilus oregonensis	*							*										*				*
Mylocheilus caurinus																		*				
Catostomidae																						
Catostomus macrocheilus				*					*				*					*				*
Ictaluridae N																						
Ictalurus nebulosus N					*														*	*		
Gasterosteidae																						
Gasterosteus aculeatus	*	*	*		*	*			*	*	*		*	*	*		*					
Percidae N																						
Perca flavescens N														*								
Centrarchidae N																						
Micropterus salmoides N				*	*		+					*		*			*	*				*
Ambloplites rupestris N				*																		
Pomoxis nigromaculatus N					*																	
Lepomis macrochirus N				*	*																	
L. gibbosus N							*	*														
Cottidae																						
Cottus confusus									*	*												
C. rhotheus	*			*							*											
C. asper							*							*								
C. gulosus	*			*		*																
Number of species in collection	10	2	2	8	5	3	4	2	6	7	6	3	2	4	2	1	2	7	2	1	4	
Number of non-native species in collection	0	0	0	3	4	0	3	1	0	0	0	1	0	2	0	0	1	1	2	1	4	
Number of native species in collection	10	2	2	5	1	3	1	1	6	7	6	2	2	2	2	1	1	6	0	0	0	

were collected frequently and exclusively in parent streams (Table 1). Several other fishes were collected infrequently but exclusively in parent streams. Among the latter was the redside shiner (*Richardsonius balteatus*), including one specimen from Palmer Creek (Similkameen drainage) having a tri-lobed caudal fin.

Discussion

A similarly lower species richness of a Florida oxbow lake compared to its parent stream was found by Beecher *et al.* (1977), who suggested that lower species richness

TABLE 2. Numbers of fishes in oxbow lakes with and without inlet streams.

Oxbow lakes with inlet streams				Isolated oxbow lakes			
n	x	s	range	n	x	s	range
			Chehalis drainage				
1	8.0	—	8	6	3.0	1.3	2-5
			Snoqualmie drainage				
2	3.0	1.4	2-4	4	2.0	0.8	1-3
			Similkameen drainage				
0	—	—	—	3	2.3	1.5	1-4
			Total				
3	4.7	3.1	2-8	13	2.5	1.2	1-5

TABLE 3. Number of fishes per seine haul in oxbow lakes and parent streams.

Oxbow lakes				Parent streams			
n	x	s	range	n	x	s	range
			Chehalis drainage				
24	2.2	1.3	1-6	8	3.2	2.2	1-7
			Snoqualmie drainage				
19	1.5	0.7	1-3	23	2.0	0.8	1-4
			Similkameen drainage				
8	1.9	1.3	1-4	5	3.0	1.6	1-5
			Total				
51	1.9	1.1	1-6	36	2.4	1.6	1-7

TABLE 4. Fish species in Chehalis basin seine collections with and without **Novumbra hubbsi.** Letter indicates native species and number indicates non-native species: A—**Entosphenus tridentatus**, B—**Oncorhynchus kisutch**, C—**Ptychocheilus oregonensis**, D—**Rhinichthys cataractae**, E—**R. osculus**, F—**Richardsonius balteatus**, G—**Catostomus macrocheilus**, H—**Cottus asper**, I—**C. gudosus**, J—**C. rhotheus**, K—**Gasterosteus aculeatus**, 1—**Cyprinus carpio**, 2—**Ictalurus nebulosus**, 3—**Ambloplites rupestris**, 4—**Lepomis gibbosus**, 5—**L. macrochirus**, 6—**Micropterus salmoides**, 7—**Pomoxis nigromaculatus.**

Location	Other native fishes present	Non-native fishes present
	Fishes collected with **N. hubbsi**	
oxbow lake 0.8 km N of Chehalis R. nr South Elma	K	—
oxbow lake 0.1 km N of Chehalis R. nr South Elma	K	—
oxbow lake nr mouth Satsop R.	I,K	—
slough at mouth of Satsop R.	C,D,E,F,I,K	—
	Fishes collected where **N. hubbsi** was not collected	
oxbow lake at Malone	A,B,E,G,I,J	2,3,5,6
oxbow lake at Ford's prairie	K	2,5,6,7
oxbow lake N end golf course, Centralia	H	1,4,(6-observed)
oxbow lake S end golf course, Centralia	C	4,(6-reported by fisherman)

was a result of lower habitat diversity in the oxbow lake. Current velocity alone has a much greater range in streams than in oxbow lakes and could account for the difference in species richness. The range of current velocities also leads to a broader range of substrates in a stream than in an oxbow lake. The greater number of species in oxbow lakes with inlet streams than in isolated oxbows supports the idea that habitat diversity affects species richness in oxbow lakes.

Lack of significant negative correlation between numbers of native and non-native fishes in Washington oxbow lakes suggests that these lakes had not reached a natural, or pre-introduction, equilibrium number of fish species, contrary to Magnuson's (1976) suggestion.

The non-native fishes which successfully invade Washington oxbow lakes are adapted to water with little or no current. Most of these fishes are native to eastern North America, where steep gradients are encountered less frequently than in western North America. In Washington state, few species are adapted to water with little or no current, and, consequently, there has been little displacement. One Washington exception to invasion or introduction without local extinction might be the Olympic mudminnow, an endemic fish of the Chehalis basin and adjacent drainage.

Do oxbow lakes, then, present examples of the filling of "vacant niches?" Hutchinson (1957) stated that "rapid spread of introduced species often gives evidence of empty niches, but such rapid spread in many instances has taken place in disturbed areas." Indeed, a totally undisturbed oxbow lake in Washington would be difficult to find. We did not sample any oxbow lakes not surrounded by farm, pasture, or golf course. The vacant niche concept is controversial (e.g., Mayr 1963: 87; Whittaker *et al.*, 1973: 333; Pianka 1978: 285), and these data do not resolve it.

The Olympic mudminnow is one of the few native fishes adapted to sluggish waters such as those in oxbow lakes. Our data suggest that mudminnows might be excluded from Chehalis drainage oxbow lakes by non-native fishes. Further studies, possibly including experimental introduction of non-native fishes into an oxbow lake containing mudminnows, or the reverse, are needed to test this hypothesis. Habitat disturbance appears inadequate to explain the absence of mudminnows from some oxbow lakes, since similar degrees of agricultural disturbance occurred at oxbow lakes with and without mudminnows.

Because of its restricted range and taxonomic uniqueness (Miller 1964), the Olympic mudminnow is considered a species of special concern by the Endangered Species Committee of the American Fisheries Society (Deacon *et al.* 1979), the Washington Department of Game, and the Washington Natural Heritage Program of The Nature Conservancy. It was listed in Threatened Wildlife of the U.S. (U.S. Office of Endangered Species and International Activities, 1973), an unofficial listing which predated the Endangered Species Act. Introduction of non-native fishes was listed as one of the threats to 24 of 34 fishes listed as endangered or threatened in the United States (Williams and Finnley 1977). A category which included introduction of non-native fishes was listed as a threat to 37 percent of 251 fish taxa listed as endangered, threatened, or of special concern in Canada, the United States, and northern Mexico, but only habitat loss was listed as a threat to the Olympic mudminnow (Deacon *et al.* 1979). However, Moyle (1976) stated that there is only limited evidence showing the direct effect of introductions on California native fishes because of the prevalence of environmental disturbances.

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Plant Communities and Elevation in a Diked Intertidal Marsh in the Coos Bay Estuary, Oregon

Abstract

Plant communities in a diked and adjacent undiked intertidal marsh were identified to investigate changes in plant community composition when an area is removed from tidal circulation. Plant community composition and elevational patterns were altered in the diked marsh as compared to the unmodified salt marsh. Only four plant species and two plant communities were common to both sites. Comparison of elevation profiles from both sites indicated the area behind the dike subsided 30-60 cm since 1914, when the dike was built. Subsidence of the land surface behind the dikes could be problematical for planners considering diked areas for natural salt marsh restoration.

Introduction

Diked intertidal lands are a common feature in many of Oregon's estuarine landscapes. Historically salt marshes, these lands have been removed from tidal influence and reclaimed for agricultural purposes by the construction of earthen dikes. As a result, these lands have experienced changes in flora and plant community composition. Despite the prevalence of diked intertidal land along the coast, little research has been conducted on the flora, plant communities, and the elevational patterns in these man-modified habitats (Ganong 1903, Roman 1978, Hoffnagle 1981, Eilers 1980). This paper describes the plant communities in a diked intertidal marsh in the Coos Bay estuary, Oregon, and presents a reconstruction of its vegetation history and elevational changes.

Study Areas

The diked marsh under study is located at the head of Joe Ney Slough in the southern arm of the Coos Bay estuary and covers 26 ha (Fig. 1). The dikes were erected in 1914 (Coos County, 1914) and were effective in removing the area from tidal influence. Disturbance of the soil surface associated with land reclamation, cropping, grazing, and forestry practices has occurred frequently since installation of the dikes (Taylor and Frenkel 1979).

The reclaimed area is predominantly level but also has numerous shallow depressions and small ridges. These are morphological remnants of the historic salt marsh drainage system and microtopography. Vegetation is dominated by emergent freshwater wetland species, and upland grasses and forbs in wet and dry sites, respectively.

In order to determine quantitatively the effects of diking on vegetation and surface elevation, an unmodified salt marsh in Joe Ney Slough, Beaver Marsh, was included in the study. This small, 0.26 ha, fringing salt marsh lies approximately 600 m west and

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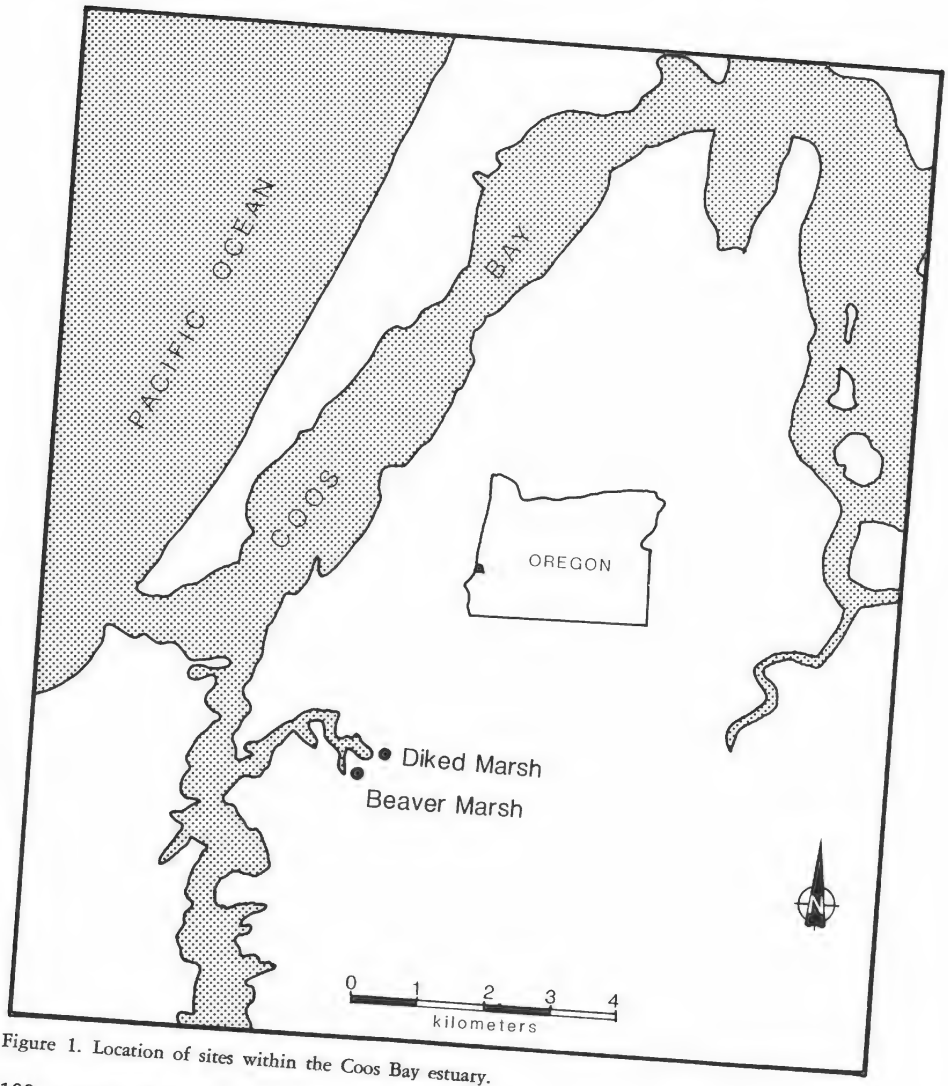

Figure 1. Location of sites within the Coos Bay estuary.

100 m south of the diked marsh (Fig. 1) and is laced with shallow tidal creeks. The marsh surface is dominated by typical salt marsh species *Salicornia virginica, Triglochin maritima,* and *Deschampsia cespitosa.* The marsh substrate is silt-based and is typical of immature high marshes in many Oregon estuaries (Jefferson 1974).

Methods

Vegetation

Vegetation in the diked marsh was sampled every 5 m along a system of 30 transects running perpendicular to the elevation gradient. At each sample point, cover class for

each species was estimated in a 20 X 50 cm plot frame (Table 1). A total of 682 cover determinations were made between June and August 1978. Plant nomenclature follows Hitchcock and Cronquist (1973).

At Beaver Marsh, ten transects perpendicular to the elevation gradient were established for vegetation sampling, and cover class recorded as above every 2 m, for a total of 71 samples.

TABLE 1. Cover class and midpoint cover values used for vegetation sampling and analysis.

Cover class	Percent cover	Midpoint value	Cover class	Percent cover	Midpoint value
1	0-1	1	7	40-50	45
2	1-5	3	8	50-60	55
3	5-10	8	9	60-70	65
4	10-20	15	10	70-80	75
5	20-30	25	11	80-90	85
6	30-40	35	12	90-100	95

Elevation

The elevation of each sample point was determined by third order levelling (Bouchard and Moffitt 1965) with reference to a tidal benchmark established at the head of Joe Ney Slough by the method of simultaneous observations (Marmer 1951). Elevations for each point were then expressed as height above Mean Lower Low Water (MLLW).

Data Analysis

Plant communities were identified by cluster analysis (Keniston 1978) of species midpoint cover class values (Table 1). By this procedure, coefficents of dissimilarity for all samples are calculated using the Bray-Curtis index and sample relationships are displayed in dendrogram form. The group average fusion strategy was chosen because it introduces relatively little distortion to the inter-entity resemblance matrix (Boesch 1977). Only species with greater than 1 percent frequency were included in the analysis.

Results

In the diked marsh, nine plant communities were identified by cluster analysis of composite vegetation samples (Fig. 2) and their elevational ranges determined

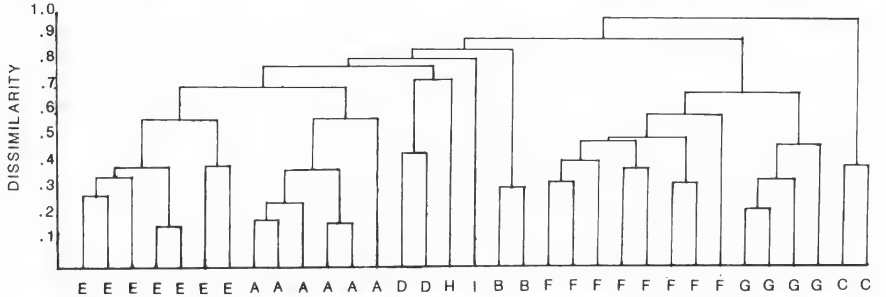

Figure 2. Dendrogram of composite vegetation samples showing plant communities in the Joe Ney Slough diked marsh. Communities identified are: A) *Eleocharis-Agrostis alba*; B) *Carex lyngbyei*; C) *Carex obnupta*; D) *Juncus effusus-Lotus corniculatus*; E) *Agrostis alba-Potentilla*; F) *Holcus-Agrostis tenuis*; G) *Agrostis tenuis-Festuca arundinacea*; H) *Oenanthe sarmentosa-Agrostis alba*; I) *Juncus balticus*.

(Table 2). A vegetation map displaying community distribution is presented in Fig. 3, and composition characteristics are summarized in Table 3. A brief description of the plant communities in order of diminishing moisture and increasing elevation is presented below.

TABLE 2. Elevational range of plant communities identified in Joe Ney Slough diked marsh. Elevations are height above Mean Lower Low Water (MLLW).

	Plant community	Elevation (m)
ElAg	**Eleocharis-Agrostis alba**	1.3-1.5/1.7-2.2
Caly	**Carex lyngbyei**	1.1-1.6
Caob	**Carex obnupta**	1.2-1.6
OeAg	**Oenanthe-Agrostis alba**	1.6-2.0
JuLo	**Juncus effusus-Lotus corniculatus**	1.7-2.2
AgPo	**Agrostis alba-Potentilla**	1.5-2.0
Juba	**Juncus balticus**	1.9-2.4
HoAg	**Holcus-Agrostis tenuis-Ranunculus**	1.9-2.6
AgFe	**Agrostis tenuis-Festuca arundinacea**	> 1.9

The *Eleocharis-Agrostis alba* community is found between the elevations of 1.3-1.5 m, and 1.7-2.2 m where standing water is an important factor determining community development. A notable characteristic of this community is the large clumps of *Juncus effusus* var. *pacificus* which often exceed 1 m in diameter. The presence of emergent aquatic plants, such as *Sparganium simplex* and *Jussiaea uruguayensis*, reflects the hydric nature of this community.

The *Carex lyngbyei* community is found between the elevations of 1.1-1.6 m in periodically inundated areas adjacent to the main creek channel. The distribution of this salt-tolerant sedge community may be influenced by seepage of saline waters through the dike and tidegate. Alkaline conditions, as indicated by pH (7.8-8.4), were identified in soil layers below 50 cm.

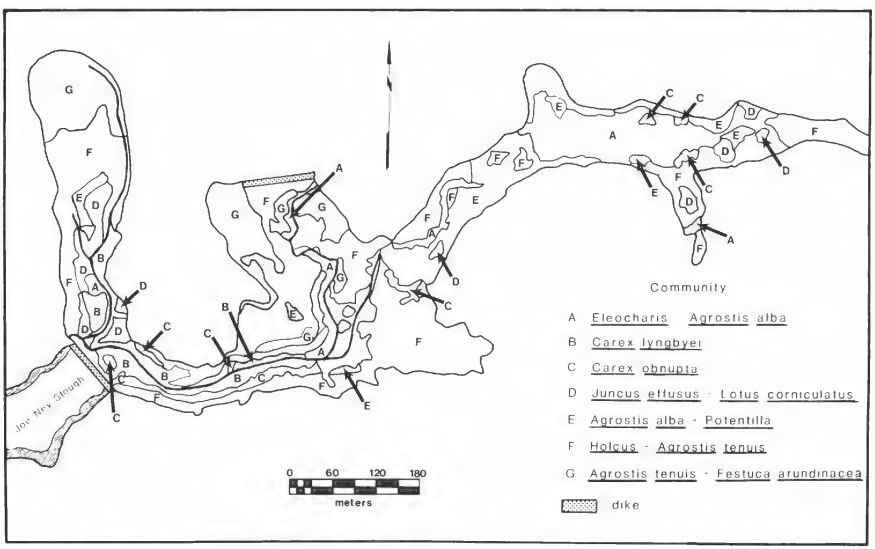

Figure 3. Vegetation of Joe Ney Slough diked marsh.

TABLE 3. Characteristics of plant communities identified in Joe Ney Slough diked marsh. Only species with five percent frequency in an identified community are listed. + = less than one percent cover. Refer to Table 1 for community acronym.

Community	ElAg		Caly		Caob		OeAg		JuLo		AgPo		Juba		HoAg		AgFe	
No. quadrats	124		59		20		14		41		151		17		164		72	
Species	Fre	Cov	Fre	Cov	Fre	Cov	Fre	Cov	Fre	Cov	Fre	Cov	Fre	Cov	Fre	Cov	Fre	Cov
Agrostis alba	80	38	46	12	30	7	79	22	37	13	97	60	41	14	44	14	26	3
Agrostis tenuis	4	1					7	+	7	1	26	3	11	5	82	41	99	64
Alopecurus geniculatus	27	6					43	16			39	16			34	8	10	1
Bromus secalinus																	12	2
Carex lyngbyei	16	2	80	58														
Carex obnupta	14	95			95	83			10	8								
Eleocharis palustris			69	21	40	4	29	6	31	9	17	5						
Epilobium watsonii					15	+	14	4	12	4								
Festuca arundinacea															11	5	50	43
Festuca bromoides																	3	+
Galium trifidum	10	1	5	+	5	+	14	+	31	5								
Glyceria occidentalis			2	1	20	1	14	3	7	1								
Holcus lanatus	7	2	3	+			14	+	43	7	32	7	11	4	84	54	50	14
Juncus balticus			13	2					7	2			53	44				
J. effusus var. **gracilis**	13	3					14	3	80	62	9	4						
J. effusus var. **pacificus**	27	15					21	20			6	2						
Jussiaea uruguayensis	8	3					7	1										
Lolium perenne			2	2													27	6
Lotus corniculatus	10	5					7	3	56	21	11	2	5	4	23	12	8	1
Oenanthe sarmentosa							64	41			8	3			6	3		
Poa palustris							28	1			10	1	11	1	21	24	29	3
Potentilla pacifica	55	17	16	2	30	2	21	4	45	13	65	31	24	10	46	20	13	3
Ranunculus repens	13	3			11	+	14	2	22	8	24	6	18	7	64	38	15	1
Rubus spectabilis							7	3										
Rumex obtusifolius							14	4							6	2	7	+
Scirpus americanus	7	1	16	1														
Scirpus microcarpus					5	5	7	5	20	16			6	2				
Sparganium simplex	11	4					7	+	10	3								
Typha latifolia			13	6														
Veronica americana	7	1			10	3	7	+										
Bare ground			9	11	25	9												

Slightly higher in elevation, 1.2-1.6 m, and adjacent to the *Carex lyngbyei* community, a *Carex obnupta* community has developed. The influence of freshwater seepage from the surrounding upland may be responsible for the abrupt boundary noted between these two sedge communities.

The *Oenanthe sarmentosa-Agrostis alba* community dominates areas with saturated organic soils along the fringes of the study area between 1.6 and 2.0 m. This community is found exclusively in the shade of the adjacent tree canopy. Frequent occurrences of *Juncus effusus* var. *pacificus, Alopecurus geniculatus*, and *Eleocharis palustris* are characteristic of this community.

The *Juncus effusus-Lotus corniculatus* community occupies transitional areas between the wet *Eleocharis-Agrotis alba* community and higher elevation grasslands. This community was found between elevations of 1.7 and 2.2 m.

Also transitionally located, the *Agrostis alba-Potentilla* community is found between 1.5 and 2.0 m. This community dominates saturated soils and contains a high frequency of *Agrostis tenuis, Holcus lanatus,* and *Ranunculus repens,* which are characteristic of more xeric upland communities.

Poorly developed in the diked marsh, the *Juncus balticus* community occurs at a few locations between the *Juncus effusus-Lotus corniculatus* community and dryer upland communities. This seasonally saturated association is confined to elevations between 1.9 and 2.4 m.

The *Holcus-Agrostis tenuis-Ranunculus* is the most extensively developed community in the diked marsh. Characteristically occupying areas 50 cm or more above the mesic grassland and wetland communities, it reaches maximum development between 1.9 and 2.6 m. Distributional pattern and geomorphic relationships indicate that this community has developed on the former salt marsh surface.

The well drained *Agrostis tenuis-Festuca arundinacea* community is found at the highest elevations above 1.9 m. The seasonally xeric nature of this community is reflected by the presence of such introduced upland meadow species as *Festuca bromoides* and *Bromus secalinus.* This community dominates areas which were formerly high salt marsh.

In general, plant communities below 1.7 m, or at higher elevations where soils are saturated, are dominated by *Eleocharis palustris, Carex obnupta, Carex lyngbyei*, and *Juncus effusus.* Higher in elevation and under dryer soil conditions, community composition changes. Dominant dry site species are *Holcus lanatus, Agrostis tenuis, Ranunculus repens*, and *Festuca arundinacea.*

Seven plant communities were identified in the Beaver salt marsh by cluster analysis (Fig. 4), their elevational range determined (Table 4), and community characteristics summarized (Table 5).

The *Salicornia* community occurs between 1.5 and 1.7 m on the seaward fringe of the marsh surface 60 cm or more above the adjacent tideflat. This community is dominated by the mat forming woody perennial *Salicornia virginica*, with frequent occurrences of *Triglochin maritima, Carex lyngbyei*, and *Deschampsia cespitosa.*

The *Carex lyngbyei* community is developed within two distinct elevational belts on this marsh. This community is dominant between 1.7 and 2.0 m, landward of the *Salicornia* community, and between 2.3 and 2.6 m where freshwater from the upland and adjacent creek influences the marsh.

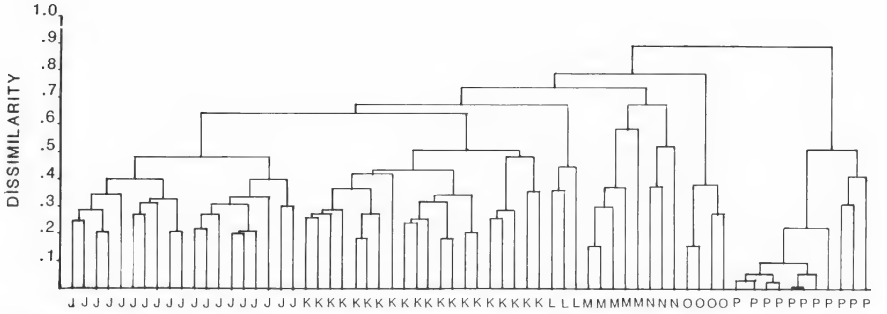

Figure 4. Dendrogram displaying sample relationships and identified plant communities in Beaver salt marsh. Communities are: J) *Juncus balticus-Agrostis alba*; K) *Deschampsia-Juncus balticus-Triglochin*; L) *Agrostis alba-Triglochin-Plantago*; M) *Potentilla-Festuca rubra*; N) *Agrostis alba-Potentilla*; O) *Salicornia virginica*; P) *Carex lyngbyei.*

The *Deschampsia-Juncus balticus-Triglochin* community is dominant between 2.0 and 2.45 m and typifies immature high marshes as described by Jefferson (1974). The high frequency of species associated with low and high marsh communities—*Salicornia virginica, Triglochin maritima, Potentilla pacifica,* and *Festuca rubra*—indicate the transitional nature of this community.

Poorly developed on this marsh, the *Agrostis alba-Triglochin-Plantago* community occurs along tidal creeks where disturbance drainage and flooding are important factors in community development.

The *Agrostis alba-Potentilla* community has developed in a few locations between elevations of 2.35 and 2.5 m. This community is comparable to the *Agrostis alba-Potentilla* community in the diked marsh where freshwater soil conditions influence community distribution.

The *Juncus balticus-Agrostis alba* community is the most extensive community on Beaver Marsh. Found between 2.35 and 2.6 m, this community corresponds well with transitional and high marsh communities identified in other Oregon and Washington estuaries (Eilers 1975, Jefferson 1974, Frenkel *et al.* 1978).

Highest on the marsh surface (2.5-2.6 m), the *Potentilla-Festuca rubra* community has developed. Freshwater seepage and infrequent submergence are important factors determining community distribution.

In summary, a stepwise elevational series of plant communities were identified on Beaver Marsh. Species tolerant of substantial periods of inundation, such as *Salicornia virginica* and *Carex lyngbyei*, dominate the lowest elevations. Community composition

TABLE 4. Elevational range of plant communities identified in Beaver salt marsh. Elevattions are height above Mean Lower Low Water (MLLW).

	Plant Community	Elevation (m)
Savi	**Salicornia**	1.5-1.7
Caly	**Carex lyngbyei**	1.7-2.0/2.3-2.6
DeJuTr	**Deschampsia-Juncus balticus-Triglochin**	2.0-2.5
AgTrPl	**Agrostis alba-Triglochin-Plantago**	
AgPo	**Agrostis alba-Potentilla**	2.3-2.5
JuAg	**Juncus balticus-Agrostis alba**	2.3-2.5
PoFe	**Potentilla-Festuca rubra**	2.5-2.6

TABLE 5. Characteristics of plant communities identified in Beaver salt marsh. Only species with five percent frequency in an identified community are listed. + = less than one percent cover. Refer to Table 2 for community acronym.

Community	Savi		Caly		DeJuTr		AgTrPl		AgPo		JuAg		PoFe	
No. quadrats	4		11		18		3		3		17		5	
Species	Fre	Cov	Fre	Cov	Cov	Cov	Fre	Cov	Fre	Cov	Fre	Cov	Fre	Cov
Agrostis alba			18	2	16	+	66	60	100	41	68	27	80	11
Aster subspicatus											6	1	20	3
Atriplex patula					26	3					23	4		
Calamagrostis nutkaensis			72	40										
Carex lyngbyei			100	87	10	1					33	5	100	27
Deschampsia cespitosa	25	2	9	+	100	55	66	17			61	17	40	14
Distichlis spicata	75	15			40	10					17	2		
Festuca rubra					60	15	100	30	33	5	50	13	100	53
Glaux maritima					47	3	66	6						
Hordeum brachyantherum											16	2		
Jaumea carnosa					5	+								
Juncus balticus	100	10	18	9	80	30	100	14	100	4	95	75	60	35
Plantago maritima					10	+	66	36						
Potentilla pacifica			18	1	70	10			100	42	72	17	100	49
Salicornia virginica	100	80			37	6								
Triglochin maritima	75	10			90	25	100	45	33	1	44	14		
Bare ground			72	40										

at higher elevations is dominated by such mid and high marsh species as *Deschampsia cespitosa, Potentilla pacifica,* and *Agrostis alba.*

Results of the elevation survey indicate that the land surface behind the dikes has subsided between 30 and 60 cm (Fig. 5). This subsidence can be attributed to decomposition and oxidation of the organic composition in the marsh soil. Compaction from vehicular traffic, associated with logging and agricultural uses, may also be important factors locally. Similar subsidence values have been reported from other tidally restricted salt marshes (Roman 1978, Eilers 1980).

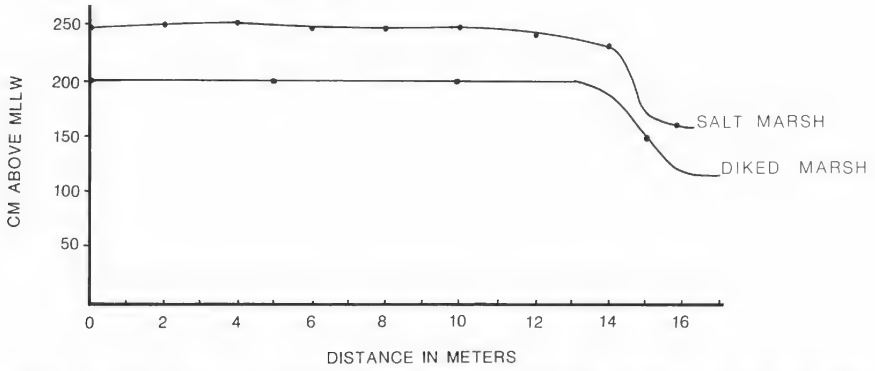

Figure 5. Elevation profile of transect 33 in Beaver salt marsh, and transect 10 in Joe Ney Slough diked marsh. Dots indicate elevation sample points.

Discussion

Diking has completely altered plant community composition of the historic salt marsh in Joe Ney Slough. This alteration can be attributed to changes in salinity regime, water table height, soil aeration, and desiccation (Beeftink 1979, Roman 1978). The trend is expressed in the replacement of halophytic plant communities by predominantly glycophytic communities. Research on alterations in similar diked marshes in Europe indicates that the significant ecological changes take place one to seven years after removal of the tidal factor (Beeftink 1979, Joenje 1978, Van Noordwijk-Puijk *et al.* 1979).

A comparison of the flora from the two sites shows only four species common to both: *Agrostis alba, Carex lyngbyei, Juncus balticus,* and *Potentilla pacifica.* Only the *Carex lyngbyei* and *Agrostis alba-Potentilla* communities are common to both sites, although their elevational ranges are significantly different (1.1-1.7 m vs 1.7-2.0 m) and (1.5-2.0 m vs 2.35-2.4 m), respectively. Additionally, 46 percent of the diked marsh flora is represented by introduced European species. The majority of introduced taxa are confined to the higher elevation grassland communities. None were identified in the unmodified salt marsh.

Pre-diking vegetation and elevation pattern can be reconstructed based on the pattern identified in the unmodified salt marsh. Prior to diking, the area was probably dominated by the *Deschampsia-Juncus balticus-Triglochin* and *Juncus balticus-Agrostis alba* communities between the elevations of 2.0-2.45, and 2.35-2.6 m. The seaward fringe of this historic salt marsh was likely dominated by the inundation-tolerant

Salicornia and *Carex lyngbyei* communities. Areas of maximum tidal submergence, below 1.4 m, were probably tidal mudflat.

The distribution of salt marsh plants is closely linked to the height of the marsh surface with respect to the tides (Chapman 1938, Hinde 1954, Adams 1963, Eilers 1975). Subsidence values measured in the diked marsh (30-60 cm) have altered this important relationship and may prove significant to planners considering these areas as habitat mitigation sites associated with estuarine development. Return of tidal contact to a southern California diked marsh, where subsidence of 80 cm was recorded, resulted in the decay and drowning of the existing salt marsh (Eilers 1980). Similar problems can be expected in returning diked intertidal lands to estuarine function in Oregon if a large amount of subsidence has occurred.

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Nitrogen Fertilization Effects on the Essential Oils in Sagebrush[1]

Abstract

Total essential oil concentrations in low sagebrush (*Artemisia arbuscula* Nutt. ssp. *arbuscula*), mountain big sagebrush (*A. tridentata* ssp. *vaseyana* (Rydb.)), and Wyoming big sagebrush (*A. tridentata* ssp. *Wyomingensis Beetle*) as influenced by N and S fertilization were examined. No significant effects were found due to large variation in oil levels between plants within a fertilizer treatment. A tendency for lower oil concentrations in fertilized mountain and Wyoming big sagebrush was evident, whereas levels of oil in low sagebrush were almost nil, regardless of treatment.

Introduction

The essential oils were the first group of secondary metabolic products in sagebrush foliage to be isolated and studied chemically (Adams and Oakberg 1934, Kinney *et al.* 1941). Monoterpenes are the major constituents in these oils, and their bacteriostatic and antibiotic effects toward rumen microbes lead investigators to suspect an ecological role for these compounds by influencing digestion and shrub consumption (Nagy *et al.* 1964; Nagy and Tengerdy 1967, 1968). In the subsequent years there has been an explosion of research (as cited by the following works) on all species of these oils: 1) their chemical makeup (Scholl 1976, Buttkus *et al.* 1977, Noble 1978, Gaudioso 1980, Welch and McArthur 1981); 2) influence on shrub palatability (Sheehy 1975, Scholl 1976) and digestion (Welch and Pederson 1981); and 3) response to environmental factors (Powell 1968).

In this article we present information on how the total concentration of essential oils in *A. arbuscula* Nutt. ssp. *arbuscula* (low sagebrush), *A. tridentata* ssp. *Wyomingensis Beetle* (Wyoming big sagebrush), and *A. tridentata* ssp. *vaseyana* (Rydb.) Beetle (mountain big sagebrush) responds to commercial fertilizer applied over a number of years.

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Methods

The Wyoming sagebrush site at 1403 m elevation was located on the Squaw Butte Experiment Station, 68 km west of Burns, Oregon. Sites supporting mountain big sagebrush at 1433 m and low sagebrush at 1403 m elevation were situated on Sagehen summit, 40 km west of Burns. Soils underlying these stands are unclassified but are sandy-loams with indurated restrictive layers cemented by siliceous materials occurring from 20-30 cm below the surface. Annual precipitation is approximately 28 cm on all sites.

The Wyoming big sagebrush site was plowed and seeded to crested wheatgrass ((*Agropyron desertorum*) [Fisch] Schult.) in 1951-1952 but was rapidly reclaimed by the shrubs. In 1971, field experiments were initiated to assess the relative competition between sagebrush and crested wheatgrass when fertilized with nitrogen and sulfur.[2] A randomized complete block design with four replications and four treatment plots (9 x 18 m) was established. Plots were fertilized in the fall as follows:

1. Four consecutive years (1971-1974) of annual applications at 22.4 kg/ha of N.
2. A single application in 1971 at 134 kg/ha of N.
3. Applications in 1971 and 1974 at 67 kg/ha of N each.
4. No fertilizer.

From 1-7 May 1975 five plants were selected at random in each treatment plot. Approximately 20 g (oven dry) of current season's growth (twig and leaf) were plucked from each shrub, sealed in plastic storage bags, and maintained in a frozen state until analyzed. Total volatile oils of each sample (twigs and leaves) were determined by steam distillation at Oregon State University (Sheehy 1975).

The mountain big sagebrush and low sagebrush sites were studied in a different time frame. Two 0.4 ha plots were established within each species during 1975 and fertilizer applied to one plot at each site as follows:

1975: 24 N - 10P - 4S (kg/ha)
1976: 18 N - 10P - 22S (kg/ha)
1977: None
1978: 30 N (kg/ha)
1979: 20 N (kg/ha)

Current season's growth of twigs and leaves (100 g) was obtained from each of three randomly selected plants in each plot from 12-18 September 1980. These tissues were loosely packed in airtight plastic freezer cartons and maintained in a frozen state. Prior to analysis the material was frozen in liquid nitrogen and gently stirred to dislodge the leaves from the twigs. The woody tissue was removed and the volatile oils in the leaves only quantified by 2 hours of steam distillation on duplicate samples (Kelsey *et al.*, in press). A small sample was used for determining leaf moisture content (oven dried at 100°C). Concentrations of oils in this report are expressed as a percent of oven dry leaf weight.

Results and Discussion

The mean concentration of volatile oils in Wyoming big sagebrush was 3.7 percent ± 1.0 percent (standard deviation) in plants from unfertilized plots and decreased to

[2] NH_4NO_3 + 6 percent sulfur.

2.3 ± 0.8, 2.9 ± 0.8, 2.8 ± 1.1 percent in plants from treatment 1, 2, and 3, respectively. However, due to the great variation in volatile oil concentrations between individual plants (ranges from 1.1 to 6.1 percent), significant differences could not be established for treatments at the 5 percent probability level. This finding supports the conclusions of Welch and McArthur (1981) that the quantity of oil is strongly influenced by genetic makeup.

Concentrations of essential oils in mountain big sagebrush were 5.4 ± 2.5 and 4.4 ± 1.5 percent of dry leaf tissue for unfertilized and fertilized plants, respectively. Significant differences between treatments were not established at the 5 percent level because of large variation for plants within a treatment with oil levels in the control group ranging from 3.0 to 8.1 percent. However, as observed in *wyomingensis*, there was a tendency for lower concentrations of oils in fertilized plants.

All *A. arbuscula* contained only trace quantities of volatile oils, regardless of fertilizer treatment. The laboratory apparatus and techniques used have previously determined levels as low as 0.5 percent oil successfully. Sheehy (1975) reported 0.0 to 0.5 percent oil concentrations in low sagebrush collected from three eastern Oregon sites. In Montana, Scholl (1976) reported summer concentrations in *A. arbuscula* to be much higher (1.71 percent).

No quantitative measurements of sagebrush growth were made; but, increased leader length, denser foliage, and increased numbers of reproductive stems were observed on fertilized plots. Thus, even though differences were not statistically significant, the lowest oil levels were associated with vegetation that had visually responded to N with increases in vegetative material, which possibly diluted the concentrations. Alternatively, monoterpenoid biosynthesis could have been reduced if the energy from available photosynthate and stored reserve compounds was channeled into primary metabolism required in the formation of the additional vegetative tissue on fertilized plants (Loomis and Croteau 1973).

Mean oil concentrations in these studies not only reflect differences among sagebrush taxa but also plant component differences. The mean concentration for Wyoming sagebrush is that representing twigs and leaves as compared with that of leaves only for mountain big sagebrush and low sagebrush. Neither the oil concentration in the two compartments nor the proportion of leaves to twig for current season growth for the different sagebrush taxa has been adequately addressed by research.

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Food Habits of the Spotted Frog (Rana pretiosa) from Managed Sites in Grant County, Oregon

Abstract

A great variety of insect food, including distasteful types, was eaten by the spotted frog (*Rana pretiosa*) in the Blue Mountains of Oregon, indicating that *pretiosa* is an opportunistic feeder. Frogs from four variously managed sites displayed different dietary habits, indicating that land management practices may have caused changes in the abundance or composition of local insect populations.

Introduction

The food habits of the spotted frog (*Rana pretiosa*) have been studied in various parts of its range (Moore and Strickland 1954, Turner 1959, Miller 1978). The present study was designed to contribute further regional information and to study possible differences in food habits among four different forest range management systems. Differences in food habits among sites reflect basic differences in availability of food that, in turn, may have been influenced by different management practices.

Study Areas

Frogs were collected at four sites in Grant County, Oregon, during July and August 1978. One pair of sites (Keeny-Clark and Flood) represented mountain-meadow habitats and the other pair (East Larch and West Larch) represented mixed conifer forest habitats. One site of each pair received intensive management, and the other was a

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control. The treated meadow habitat received numerous improvement practices, such as herbicide and fertilizer treatments, grass and legume seeding, and rodent control. The pine forest-range had overstory tree removal and timber thinning. The names, locations, and characteristics of the sites were:

Keeny-Clark

The study site is at the confluence of two meadows (Keeny and Clark) and tributaries to the south of Long Creek, 1652 m elevation. Most frogs were collected immediately south (upstream) of where USFS Rd. 1136 (T11S, R31E, S15) crosses Long Creek. The stream is somewhat intermittent, forming isolated pools in late summer. There is evidence of extensive bank erosion brought on by years of heavy cattle and sheep grazing. By late summer the pools take on a muddy and stagnant quality. The surrounding meadow is considered to be intensively managed, including reseeding and herbicide treatment. The grazing pattern is on a rotating schedule, which included no grazing in 1977 and late grazing, beginning 15 September 1978.

Flood

This study site is located just south (upstream) of USFS Rd. 1136 (T11S, R31E, S11) on a tributary of the middle fork of Long Creek, 1567 m elevation, as it emerges from a large meadow (Flood). The creek and surrounding meadow are relatively undisturbed. The clear water flows all summer long, and the banks are heavily vegetated. Management of the surrounding meadow is restricted to controlled livestock grazing. Grazing is on a rotating schedule, which included late grazing in 1977; no grazing in 1978; and early grazing starting 12 June 1979.

East Larch

This site was located southwest of Fox (T12S, R30E, S5) at 1463 m elevation. The collecting site consisted of a small pond, approximately 10 m in diameter, in a draw at the west end of a large meadow. The pond is surrounded on three sides by mixed conifer forest and is protected with shrub and tree vegetation. The forest to the north of the pond was thinned in 1977 on the eastern half and in 1978 on the western half. The slash was piled and burned in the winter of 1978-79. The entire area was grass seeded.

West Larch

This site is located (T11S, R29E, S35) 5.6 k west of the East Larch site, at 1402 m elevation. It consists of a 10 x 15 m artificial pond fed by a very small intermittent stream. A large meadow is situated to the east, and mixed coniferous forest borders the other three sites. There are large stumps in the forest indicating past logging, but there are several large *Pinus ponderosa* in the immediate vicinity of the pond. There is no active timber management or harvest in the surrounding area, which is currently used for cattle grazing. The pond is relatively open around the edges and has a thick blanket of algae that covers about 50 percent of the surface. This algal mat provides excellent cover and feeding sites for frogs.

Methods

Frogs were captured with hand-dip nets. To avoid sacrificing animals, a method similar to that used for fish (Meehan and Miller 1978), turtles (Legler 1977), and lizards and

amphibians (Legler and Sullivan 1979) was used to obtain dietary samples. A 5 mm diameter glass or rigid plastic tube, attached to a 50-cc syringe, was inserted through the mouth into the stomach of the frog and the contents simply flushed back out through the relatively short esophagus by forcing water into the stomach. The food fragments were separated from the flush water by straining through gauze, and its contents were placed in 10 percent formalin or 70 percent ethyl alcohol for preservation. The frogs were branded with hot chromel wire (Clark 1971) and returned to their habitat for continued diet sampling and capture-recapture population estimates.

Results and Discussion

A large variety of food was eaten by spotted frogs (Table 1). A total of 98 food categories was represented: 49 at Flood, 43 at Keeny-Clark, 51 at West Larch, and 51 at East Larch. The majority of the food was insect material, 73 categories representing 90.7 percent of the food by volume. Other invertebrates formed seven categories, and plant material formed three categories, representing 3.9 percent of the volume. Insignificant categories were bird feathers and shed frog skins. Most sampled items were terrestrial, but a few forms were aquatic, including mayfly naiads, larval trichopterans, tipulid larvae, clams, and *Daphnia.*

Major food categories (those comprising over 5 percent volume) are listed by order of decreasing volume for each of the four areas (Table 2). There was great variation. Only one item, adult moths (Lepidoptera) occurred as a major item in stomachs from all four sites (Table 2), ranging in volume from 6.1 (Flood) to 14.5 (East Larch). Two foods occurred in stomachs from two sites: ants (Formicidae) from Flood and East Larch, and grasshoppers (Acrididae) from Flood and Keeny-Clark. A total of 13 food categories appear in this table, but nine of them occurred at only one site as major foods: water striders (Gerridae), craneflies (Tipulidae), and soldier flies (Tachinidae) at Flood; hover flies (Syrphidae), spider (Araneae), and diving beetles (Dytiscidae) at Keeny-Clark; long-legged flies (Dolichopodidae) and wasps (Vespidae) at West Larch; and caddisflies (Trichoptera) and millipedes (Diplopoda) at East Larch. Also, the food in greatest volume differed (and was in a different order) in each case.

The great variety of food items consumed by *pretiosa* in Grant County is consistent with findings of Miller (1978), from western Montana, for the same species. Assuming that frog diet reflects abundance and diversity of available prey, as demonstrated by Whitaker (1961) and Turner (1960), the great differences among the four study sites is of special interest.

The study sites were initially selected because of differences in application of range and forest management practices. Keeny-Clark and Flood Meadows are relatively close together and similar in habitat characteristics (slope, exposure, elevation, proximity to forest), as are East and West Larch sites. The intensity and type of management is clearly different at each of the sites. However, owing to lack of replication and knowledge of insect habitat requirements, it is impossible to determine whether some of the differences are related to natural habitat differences or to land management activities. In a few cases—e.g., grasshoppers—the quantity of food items selected appears to indicate past management activities. Acrididae made the greatest contribution in the Keeny-Clark (20.5 percent) and Flood (8.8 percent) meadow sites and least contri-

TABLE 1. Food of spotted frogs, **Rana pretiosa**, from four localities in Grant County, Oregon.

	Meadow				Forest				Summarized Grant County data	
	Flood		Keeny-Clark		West Larch		East Larch			
	n = 50		n = 50		n = 54		n = 52		n = 206	
	Percent		Percent		Percent		Percent		Percent	
	Volume	Frequency	Volume	Frequency	Volume	Frequency	Volume	Frequency	Volume	Frequency
Diptera										
Tipulidae—adult	7.2	28.0	0.7	2.0	3.2	9.3	2.4	11.5	3.4	12.6
Tachinidae	6.5	12.0							1.6	2.9
Dolichopodidae	4.6	14.0	0.7	10.0	10.9	51.9	1.0	9.6	4.4	21.8
Syrphidae	3.9	12.0	18.9	32.0	0.6	3.7			5.7	11.7
Acalypterata	0.9	8.0	0.2	4.0	0.7	7.4	3.6	13.5	1.4	8.3
Bombyliidae	0.6	4.0							0.15	1.0
Culicidae	0.4	4.0							0.2	1.5
Calliphoridae			1.3	8.0	0.7	1.9			0.5	2.4
Anthomyiidae			0.8	8.0	1.6	9.3	1.1	3.8	0.9	5.3
Tipulidae—larvae			0.7	6.0	0.3	1.9	4.6	15.4	1.4	5.8
Pipunculidae			0.2	2.0					0.05	0.5
Conopidae			0.1	2.0					0.02	0.5
Tabanidae (**Chrysops**)			0.1	2.0					0.02	0.5
Otitidae					1.2	7.4	0.1	1.9	0.3	2.4
Muscidae					0.8	1.9			0.2	0.5
Sarcophagidae					0.5	1.9			0.1	0.5
Simuliidae					0.1	1.9			0.02	0.5
Asilidae							2.4	17.3	0.6	4.4
Chironomidae							1.0	5.8	0.24	1.5
Stratiomyid larvae							0.5	1.9	0.12	0.5
Mycetophilidae							0.4	1.9	0.09	0.5
Dipterous larvae					0.6	3.7			0.17	1.0
Unidentified Diptera	2.9	10.0	1.1	10.0	3.3	16.7	2.5	13.5	2.5	12.6
Coleoptera										
Staphylinidae	3.7	10	0.9	6	0.1	1.9			1.1	4.4
Carabidae	1.6	10	1.5	2	0.4	3.7	0.9	7.7	1.1	5.8
Cantherid larvae	2.1	10							0.5	2.4
Cerambycidae	1.2	2					1.9	1.9	0.8	1.0
Tenebrionidae	1.0	6	1.0	2			4.3	11.5	1.6	4.9
Dytiscidae	0.8	2	5.9	16			2.5	11.5	2.3	7.3
Dytiscid larvae	0.2	2	0.3	2					0.1	1.0
Curculionidae	0.4	4	0.5	2	0.3	1.9	0.4	1.9	0.4	2.4
Chrysomelidae	0.3	4	0.4	2					0.6	1.5
Coccinellidae	0.3	2	0.6	4	0.4	1.9			0.3	1.9
Scarabaeidae	0.2	2							0.50	0.5

Scarabid larvae							0.3	1.9	0.07	0.5
Elateridae	0.1	2			0.1	1.9			0.05	1.0
Haliptidae			0.6	2			0.1	1.9	0.2	1.0
Buprestidae					0.3	1.9			0.07	0.5
Cleridae					0.3	1.9			0.07	0.5
Alleculidae					0.2	1.9			0.05	0.5
Bostrichidae							0.1	1.9	0.02	0.5
Coleopterous larvae					0.4	3.7			0.1	1.0
Unidentified Coleoptera	1.4	6	1.2	8	1.0	11.5	1.2	11.5	1.2	9.2
Isoptera	0.4	4							0.1	1.0
Hymenoptera										
Formicidae	5.1	28	2.9	22	0.3	1.9	9.6	46.2	4.4	24.3
Vespidae	0.7	2	1.0	4	31.1	57.4	3.1	5.8	9.3	18.0
Sphecidae	0.6	2	0.2	2	3.5	11.1	0.8	3.8	1.3	4.9
Apoidae	0.5	2	3.5	6	1.3	3.7			1.3	2.9
Ichneumonidae	0.1	2			0.6	3.7			0.2	1.5
Chrysididae							1.0	1.9	0.2	0.5
Apidae							0.7	1.9	0.2	0.5
Unidentified Hymenoptera	3.6	20	1.3	6	4.3	20.4	7.2	19.2	4.1	16.5
Hemiptera										
Gerridae	8.9	18	2.3	14	2.6	9.3	3.7	11.5	4.3	13.1
Corixidae	0.2	2			0.1	1.9			0.1	1.0
Reduviidae	0.2	2	1.0	2			0.4	1.9	0.4	1.5
Coriscidae			0.3	4					0.1	1.0
Miridae							0.7	1.9	0.2	0.5
Pentatomidae							0.7	1.9	0.2	0.5
Notonectidae							0.6	1.9	0.2	0.5
Unidentified Hemiptera	0.3	2					0.3	1.9	0.1	1.0
Homoptera										
Cicadellidae	0.4	4			0.5	5.6	1.0	7.7	0.5	4.4
Aphididae	0.1	2							0.02	0.5
Cicadidae			0.8	2			0.2	1.9	0.2	1.0
Fulgoridae			0.3	2					0.07	0.5
Unidentified Homoptera							0.2	1.9	0.05	0.5
Orthoptera										
Acrididae	8.8	14	20.5	28	0.6	3.7	1.2	1.9	7.6	11.7
Tetrigidae	2.0	2							0.5	0.5
Gryllidae	0.8	2	0.3	2					0.3	1.0
Tettigoniidae			0.4	2					0.1	0.5
Gryllotalpidae							0.2	1.9	0.05	0.5
Unidentified Orthoptera					0.9	3.7			0.2	1.0

Lepidoptera										
Adult	6.1	14	10.0	20	9.1	22.2	14.5	26.9	10.0	29.0
Larval	3.8	12			1.1	5.6	2.0	5.8	1.7	5.8
Trichoptera										
Adult	4.6	16	2.7	8	0.3	1.9	5.9	17.3	3.3	10.7
Larval					0.3	1.9	0.3	1.9	0.6	1.0
Odonata										
Dragonfly (Anisoptera)	3.2	4			1.7	1.9			0.8	1.0
Damselfly (Zygoptera)	0.9	2	3.4	6	0.6	1.9			1.0	2.0
Neuroptera										
Myrmeleontidae larvae	0.2	2			0.7	3.7			0.2	1.5
Hemerobiidae							0.3	1.9	0.02	0.5
Unidentified larvae					0.1	1.9			0.07	0.5
Plecoptera	0.2	2							0.05	0.5
Ephemeroptera naiad							0.1	1.9	0.02	0.5
Unidentified insects	2.7	12	0.5	4	1.3	13	3.1	13.5	1.9	10.7
Spiders	3.8	28	7.2	22	1.7	3.7	3.4	11.5	4.0	16.0
Chilopoda			0.1	2	0.2	1.9			0.07	1.0
Diplopoda					0.4	1.9	2	5.8	0.6	1.9
Snail	0.4	6							0.1	1.5
Clam							0.1	1.9	0.01	0.5
Daphnia					0.4	1.9			0.1	0.5
Frog			2.9	6					0.7	1.5
Bird Feathers							0.2	1.9	0.05	0.5
Shed Skin			0.4	2					0.1	0.5
Vegetation										
Algae	0.1	2			0.6	1.9			0.2	1.0
Grass seeds					2.5	14.8	0.5	9.6	0.6	3.9
Carex seeds					0.5	7.4			0.3	4.4
Grass stems							0.3	1.9	0.1	0.5
Leaves and stems							4.7	19.2	1.2	4.9
Unidentified vegetation	1.1	10	0.4	4	4.4	22.2			1.5	9.2
	100.1		100.1		99.7		100.3		100.3	

TABLE 2. Major foods of spotted frogs at four localities (given in percent volume).

Flood		Keeny-Clark		West Larch		East Larch	
Gerridae	8.9	Acrididae	20.5	Vespidae	31.1	Lepidoptera	14.5
Acrididae	8.8	Syrphidae	18.9	Dolichopodidae	10.9	Formicidae	9.6
Tipulidae	7.2	Lepidoptera	10.0	Lepidoptera	9.1	Trichoptera	5.9
Tachinidae	6.5	Spiders	7.2			Diplopoda	5.8
Lepidoptera	6.1	Dytiscidae	5.9				
Formicidae	5.1						

bution in the East Larch (1.2 percent) and West Larch (0.6 percent) forest sites. Dempster (1963) reported that grasshoppers and certain other ovipositing Orthoptera require compacted soil for successful reproduction. Because of preferred livestock forage on meadows, soils there have been exposed to greater trampling compaction than soils in the forest sites, clay content notwithstanding. Similarly, the intensively managed sites of both meadow and forest habitats (Keeny-Clark and East Larch) had more grasshopper food items than their counterpart control sites (Flood and West Larch).

Assuming that management activities have an effect on diet available, some additional observations can be made. The diet of Keeny-Clark frogs contained a few food types, whereas that from Flood contained a greater variety in much smaller amounts. Also, the proportion of grasshoppers (Acrididae) and hover flies (Syrphidae) in the diet is much greater at the Keeny-Clark site. The intensive use and manipulation of Keeny-Clark may have led to a decrease in plant variability with corresponding increases in the proportion and number of a few insect species adapted for exploiting such conditions. The Flood site, with less past grazing use and current manipulation, has more luxuriant vegetation and a great variety of plants. Thus, stomach data indicate the resulting insect fauna is also varied, with no groups clearly dominating.

The differences in diets of frogs from the East and West Larch forest sites is more difficult to attribute, hypothetically, to specific management practices. In fact, differences in diet here may more clearly reflect natural site variability than differences caused by manipulation. West Larch, the control site, was an artificial pond fed by intermittent runoff in an otherwise dry, open savanna forest. Vegetation surrounding the pond was sparse. East Larch, on the other hand, was a natural pond along a mostly perennial watercourse. Surrounding vegetation was diverse and abundant. These site differences probably explain the greater variety and smaller amounts of invertebrate food items at East Larch than at West Larch.

The feeding habits described herein suggest that *pretiosa* is opportunistic in the taking of prey. That frogs consumed prey items usually shunned by insect predators when other items were available lends further support to this idea. Most noticeable among these prey were the water striders (Gerridae), taken at Flood; and the wasps, yellowjackets, and hornets (Vespidae), taken at West Larch. If the frogs are random samplers of the insects using a particular site, they can provide information on the changes in invertebrate, especially insect, populations brought about by man-made environmental changes.

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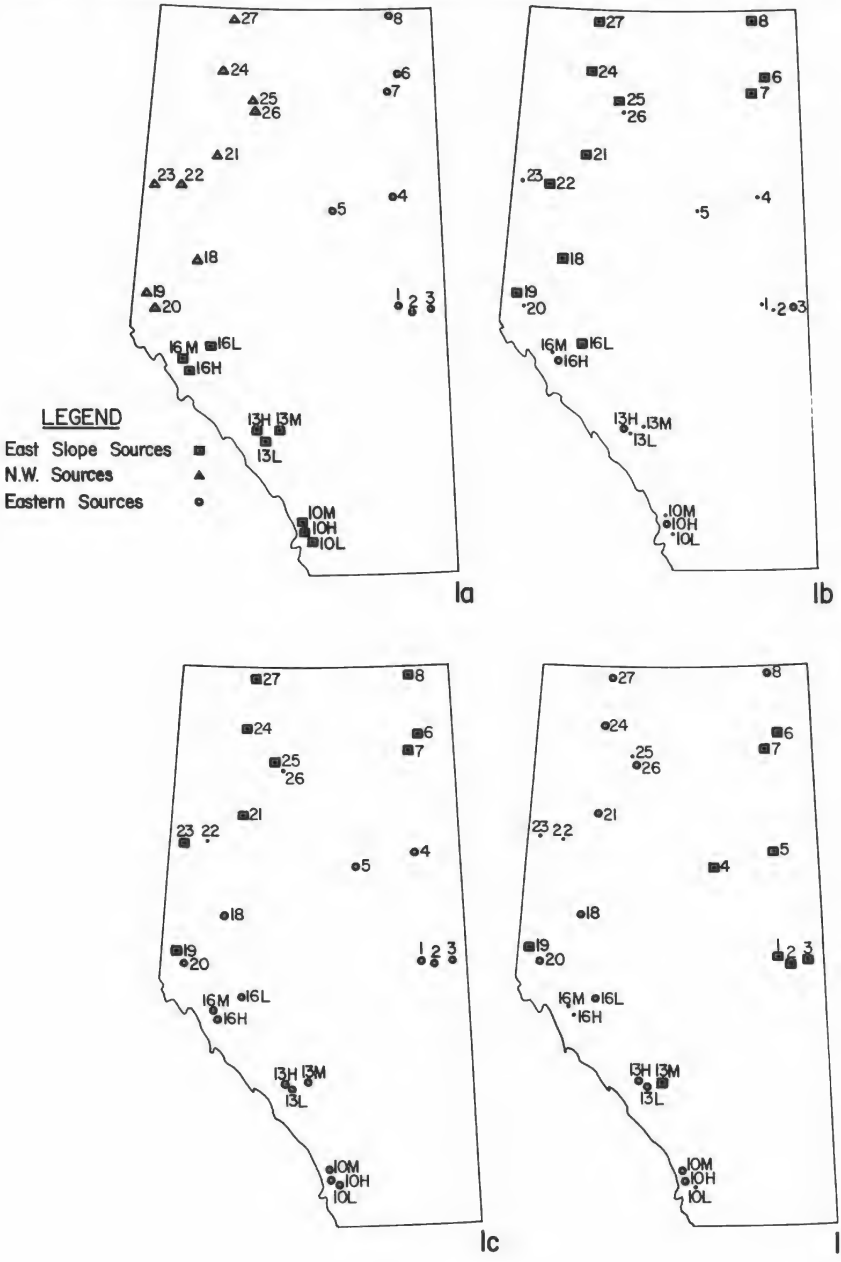
Page 75: Replace the single map in Figure 1 by the four shown below.



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Effects of SO_2 on the Lichen Flora in an Industrial Area Northwest Whatcom County, Washington

Abstract

Epiphytic foliose and fruticose lichens were systematically sampled at 20 sites in the vicinity of and generally downwind from the Atlantic Richfield (ARCO) Refinery in northwestern Whatcom County, Washington. Lichen cover and frequency were determined on ten-year-old segments of red alder (*Alnus rubra*) branches. Also, thalli of the lichen, *Hypogymnia physodes* (when available) and alder leaves were collected at each site and analyzed for total sulfur concentrations and sulfur isotope (^{34}S) values. The results showed an increase in lichen cover with an increase in distance from ARCO and an absence of highly sensitive lichens at critical locations. Total sulfur concentration in materials was also negatively correlated with distance from ARCO, and positive values of the sulfur isotope indicate that the principal source of sulfur being absorbed by alder and lichens is from fossil fuel combustion. However, the results and their interpretation are complicated by the presence of other industries and pollutants in the area.

Introduction

Sulfur dioxide is the most serious pollutant of industrialized nations. Over the last few decades, the toxicity of SO_2, especially to plants, has been documented by numerous studies. For example, the "preliminary bibliography" of Liggon and Lauenroth (1980) contains 1730 citations of articles dealing with the ecological impact of atmospheric sulfur. Recently acid rain, to which SO_2 is a major contributor, has been viewed as a serious threat to the environment.

Included among the most sulfur-sensitive organisms are various species of lichens. The importance of lichens as bioindicators, "litmus for air pollution," was summarized by Hawksworth (1971). Some points that he made that are especially pertinent to our study are: (1) air pollution and not humidity determines lichen distribution in urban and industrial areas; (2) SO_2 and not smoke is the principal pollutant; (3) lichens accumulate SO_2 in ratios directly proportional to atmospheric concentrations; (4) epiphytic lichens are the best SO_2 indicators; and (5) SO_2 tolerance among lichens is greatest in crustose forms and least in fruticose forms. In pollution studies, lichens serve as three types of bioindicators (Grodzinski and Yorks 1981): (1) scale indicators, in that the level of SO_2 can be related to the presence or absence of sensitive species; (2) true indicators, in that SO_2 dosage can be directly related to physiological and/or morphological symptoms; (3) accumulator species, in that lichens freely accumulate SO_2. Because of those bioindicator properties, lichens have been used extensively and effectively to map concentrations of SO_2 around urban and industrial centers (Gilbert 1965, 1970; Hawksworth and Rose 1970; LeBlanc and DeSloover 1970; Denison and Carpenter 1973; O'Hare 1974; Vick and Bevan 1976; Johnson 1979; Case 1980; and

others). The correlated response of lichen growth and SO_2 concentration relates to the ease with which SO_2 is absorbed by the non-cutinized lichen thallus with consequential damage, especially to the lichen algae (see, for example, Rao and LeBlanc 1966, and Ferry *et al.* 1973).

In northwestern Whatcom County, Washington, there are three major SO_2-emitting industries, the Mobil and Atlantic Richfield (ARCO) oil refineries and an aluminum reduction plant, Intalco. Previous studies within the affected area have indicated that vascular plants, bryophytes, and lichens have been damaged by SO_2 pollution (see Taylor 1978). However, no previous quantitative analyses of the lichen flora have been made. This study, then, was designed to relate the coverage and diversity of lichens to distance and direction from an SO_2 source, ARCO, and to determine the extent to which the lichen flora was altered by SO_2 emission below accepted critical levels.

Study Area

The study area was located in the vicinity of and generally downwind from the Atlantic Richfield (ARCO) Refinery near Birch Bay, a few km south of the Canadian border (Fig. 1). The two other industries in the region, Intalco Aluminum Corp. and Mobil Oil, are located ca 4 and 6 km southeast of ARCO, respectively. The area surrounding ARCO is predominantly farmland and pasture, with scattered stands of mixed conifer-hardwood trees. The terrain is of low relief, not greatly affecting wind patterns. A maritime climate predominates, with prevailing winds from the south and west (Fig. 2).

Methods and Materials

Sampling Format and Procedures

Using ARCO as a point source, the area was divided into five 30° azimuths, from 0° to 150°, which were labeled A-E, respectively. Five concentric lines were then drawn at 1 km intervals beginning at the ARCO effluent stacks. Within each intergrid space, beyond the 1 km arc, a study site was established. The resulting 20 sites were located as near the center of respective spaces as the availability of the selected lichen substrate (alder trees) allowed. The experimental design with study site locations is shown in Figure 1.

At each selected site of red alder (*Alnus rubra* Bong) groves, two peripheral trees fully exposed to the ARCO effluent were arbitrarily chosen for epiphytic lichen sampling. From each of the two trees, two live branches were collected, one facing ARCO, the other directed toward the prevailing wind, southward. Thus, a total of 80 lichen plots (branches) was sampled, four from each study site. To avoid inconsistencies associated with successional changes of the lichen flora, the branches were aged and lichen coverage values were determined for the entire circumference of the tenth-year segment. The cover class system of Daubenmire (1959) was used. Lichen nomenclature followed Hale (1969). Collections were made during the summer of 1978.

Sulfur Analyses

Total sulfur and isotopic sulfur analyses were made of 6-8 alder leaves and *Hypogymnia physodes* thalli collected from exposed branches of the trees selected for lichen coverage determinations. *Hypogymnia* was chosen as the lichen representative because of its prevalence throughout the study area, its wide use in pollution studies (Hawksworth

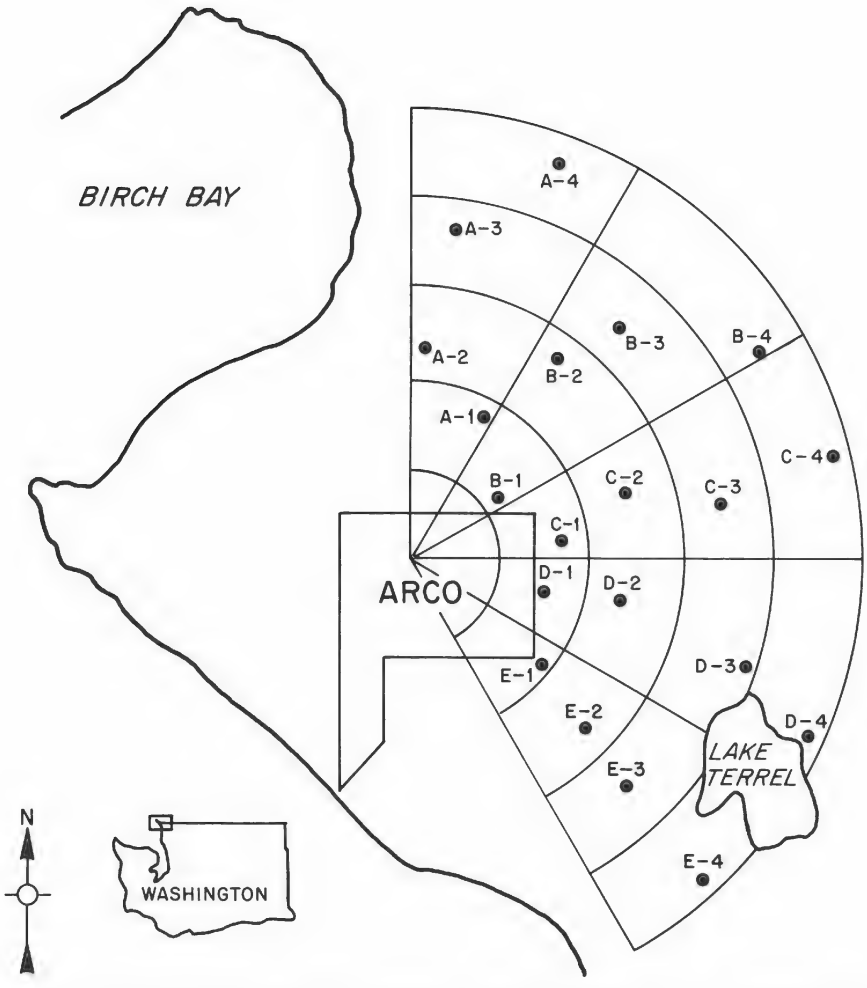


Figure 1. Study area and sampling site locations in five 30° azimuths (A-E). Concentric arcs are in 1 km increments.

and Rose 1970, Vick and Bevan 1976, Case 1980, and others), and its moderate tolerance to sulfur (Hawksworth and Rose 1970, 1976; O'Hare 1974). Chemical analyses were done in the laboratory of H. R. Krouse, University of Calgary, Alberta, Canada.

Total sulfur content of alder leaves and lichen thalli was determined using the Parr bomb and Ba^{++} titration technique outlined by Krouse (1978). Values derived were converted to parts per million (ppm) on a dry wt basis. Sulfur isotope (^{34}S) abundance was determined by mass spectrometry (Krouse 1978) and has been expressed as a delta value (δ) according to the formula (Krouse 1977):

$$\delta^{34}S = \left\{ \frac{[^{34}S/^{32}S]\ \text{sample}}{[^{34}S/^{32}S]\ \text{meteorite}} - 1 \right\} \times 1000$$

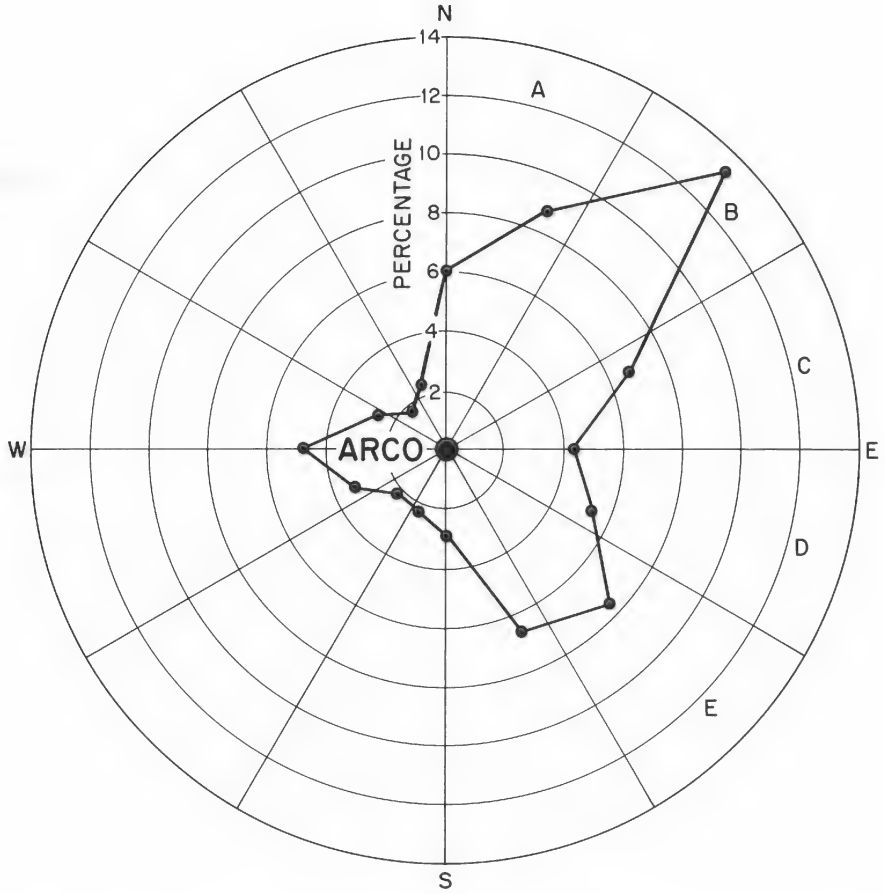


Figure 2. Wind rose, showing percentage directional (16 point) frequency of surface winds for 1978, computed on an hourly basis (data from Northwest Air Pollution Authority, unpublished). The five 30° azimuths in which sampling sites were located are identified, A-E.

Positive delta values suggest SO_2 pollution from burning of fossil fuel, i.e., sulfur-containing deposits of the Devonian Period, are especially rich in ^{34}S isotope (Krouse and Case 1981). In the above formula, meteoritic triolite is used as a standard.

Results and Discussion

Lichen Coverage

The mean cover values of lichens on source-facing and south-facing branches were not significantly different for any given study site and are therefore combined in Table 1. This lack of distinction is consistent with the findings of Vick and Bevan (1976), that lichen zonation is little affected by small climatic differences.

TABLE 1. Mean percent cover of lichens on alder branches.

Species	Azimuth (A-E) and Distance (1-4 km) from ARCO																			
	A				B				C				D				E			
Species	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Hypogymnia physodes	<1	2	9	23	3	2	6	8	3	2	6	3	1	15	3	3	2	1	12	21
Parmelia sulcata	—	2	9	12	3	9	15	32	3	6	3	33	2	44	9	3	2	3	12	12
Parmelia subaurifera	—	1	6	2	1	6	6	3	—	5	6	3	1	6	3	3	—	1	9	9
Evernia prunastri	—	—	—	1	—	—	—	—	—	2	1	—	—	1	—	1	—	—	1	3
Usnea subfloridana	—	—	1	1	—	1	—	—	—	1	<1	—	—	1	3	—	—	—	2	1
Bare bark	99	97	78	74	98	87	71	53	90	79	83	55	96	39	56	90	98	97	83	72

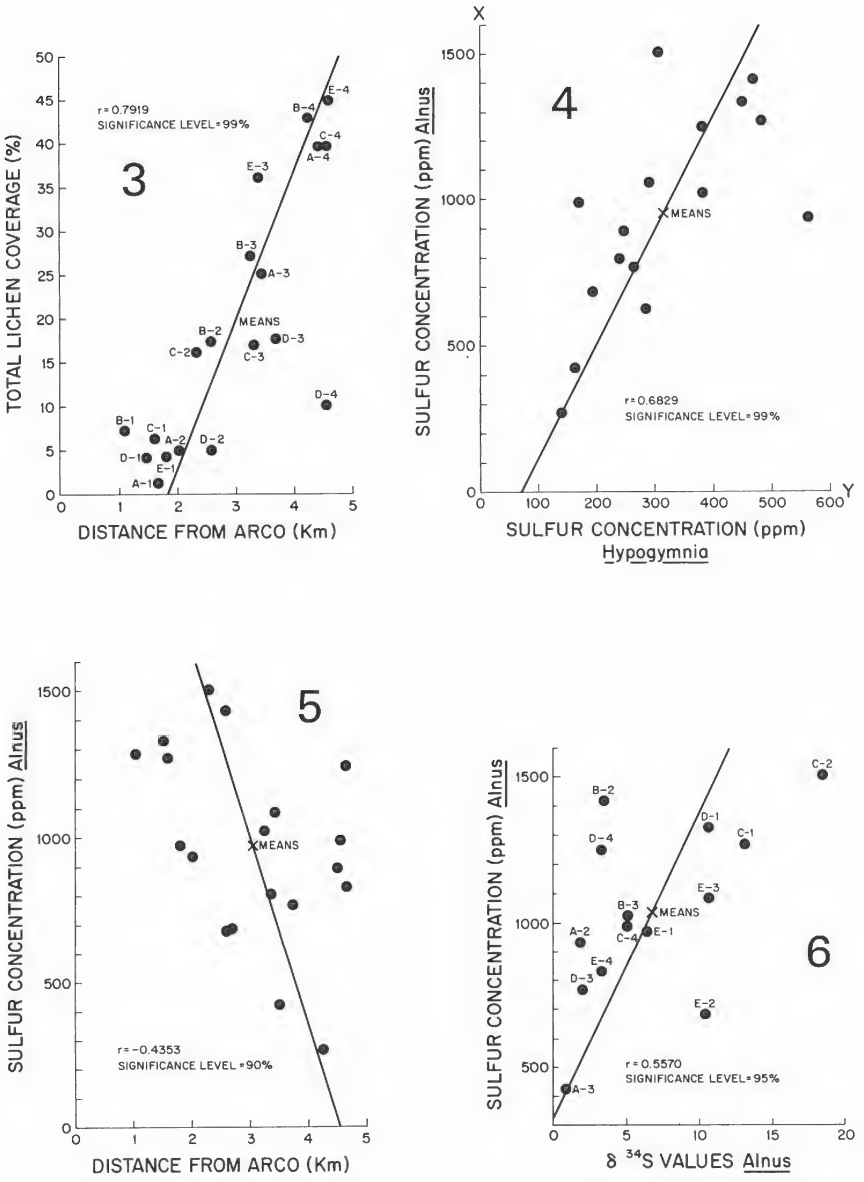
Previous researchers have cited *Hypogymnia physodes, Parmelia sulcata, Evernia prunastri,* and *Usnea subfloridana* as good bioindicators of SO_2 pollution. These species can be ranked on the basis of their SO_2 sensitivity by considering the results of Hawksworth and Rose (1970), O'Hare (1974), and Johnson (1979) in combination. *Hypogymnia* is moderately tolerant, being able to withstand ambient air SO_2 concentrations up to ca 125 $\mu g/m^3$. *Parmelia* is somewhat more sensitive, tolerating concentrations up to ca 70 $\mu g/m^3$. *Evernia* is sensitive (no tolerance values provided) and *Usnea* is highly sensitive, persisting only below SO_2 levels of 40 $\mu g/m^3$. At SO_2 levels above 150-170 $\mu g/m^3$, lichens generally do not survive (Hawksworth and Rose 1970, Vick and Bevan 1976).

These findings are consistent with data presented in Table 1, in which lichen species are listed according to their SO_2 tolerance as determined by the relationship between coverage and distance from ARCO. No distinction could be made, however, between tolerance of *Evernia* and *Usnea.* Linear regression analyses showed that, at the 95 percent confidence level, there was a functional relationship between distance from ARCO and total lichen coverage (Fig. 3) and distance vs. coverage of *H. physodes* and of *P. subaurifera. Parmelia sulcata* showed a significant relationship if the high coverage value of site D-2 were discarded. The other two lichens occurred too infrequently to show a significant correlation with distance. However, the trend toward greater cover values at greater distances can be recognized from Table 1. There was no significant relationship between annual wind directional frequency (as shown in Fig. 2) and lichen coverage at the 95 percent confidence level.

Sulfur Accumulation

Total sulfur concentrations in alder leaves varied from 267 ppm at site B-4 to 1507 ppm at site C-2, with a mean of 971 ppm. The latter is much lower than the mean value of 1817 ppm reported by Taylor (1978) for alder leaves collected in the ARCO area in 1976. During the same period (1976-1978) there was also a considerable reduction in SO_2 emission from ARCO (Northwest Air Pollution Authority, unpub. data). This fact strongly suggests that the correlation between lichen growth and distance from ARCO (Fig. 3) was more or less established during earlier periods of greater ambient SO_2 levels. Total sulfur concentration in lichen thalli (*Hypogymnia physodes*) ranged from 139 ppm, also at site B-4, to 1204 ppm at site D-1. However, at four sites there was insufficient lichen material to run sulfur analyses. Because of this paucity of data, and since sulfur concentrations in alder leaves were functionally related to those of lichen thalli at the 99 percent confidence level (Fig. 4), only values derived from alder were used in further regression analyses.

The sulfur concentration in alder leaves decreased as distance from ARCO increased (Fig. 5), but the negative relationship was not significant at the 95 percent level. Also, there was no significant relationship between sulfur concentration and wind directional frequency. This lack of correlation was at least partly due to SO_2 sources (Mobil Oil and Intalco Aluminum Corp.) southeast of ARCO, resulting in high sulfur concentrations in the C, D, and E azimuths (see Fig. 1). This finding is in accord with the Northwest Air Pollution Authority (unpub. data), which showed critical SO_2 ambient levels around, north, and east of Intalco. Interestingly, the highest isotopic delta values occurred immediately east and southeast of ARCO (see Fig. 6). Finally, there was a



Figures 3-6. Linear regression analyses. Figure 3—regression of lichen coverage with distance from ARCO. Figure 4—regression of total-sulfur concentrations in alder leaves with that of lichen thalli. Figure 5—regression of total-sulfur concentration in alder leaves with distance from ARCO. Figure 6—regression of total-sulfur concentrations in alder leaves with sulfur isotope values.

functional relationship between sulfur concentration and isotopic delta values, as shown in Figure 6, indicating that the source of excess sulfur was industrial emissions from fossil fuel combustion. The pattern of sulfur accumulation in the ARCO area was mapped by a computer graphics system (SYMAP) and is shown as an isopleth in Figure 7.

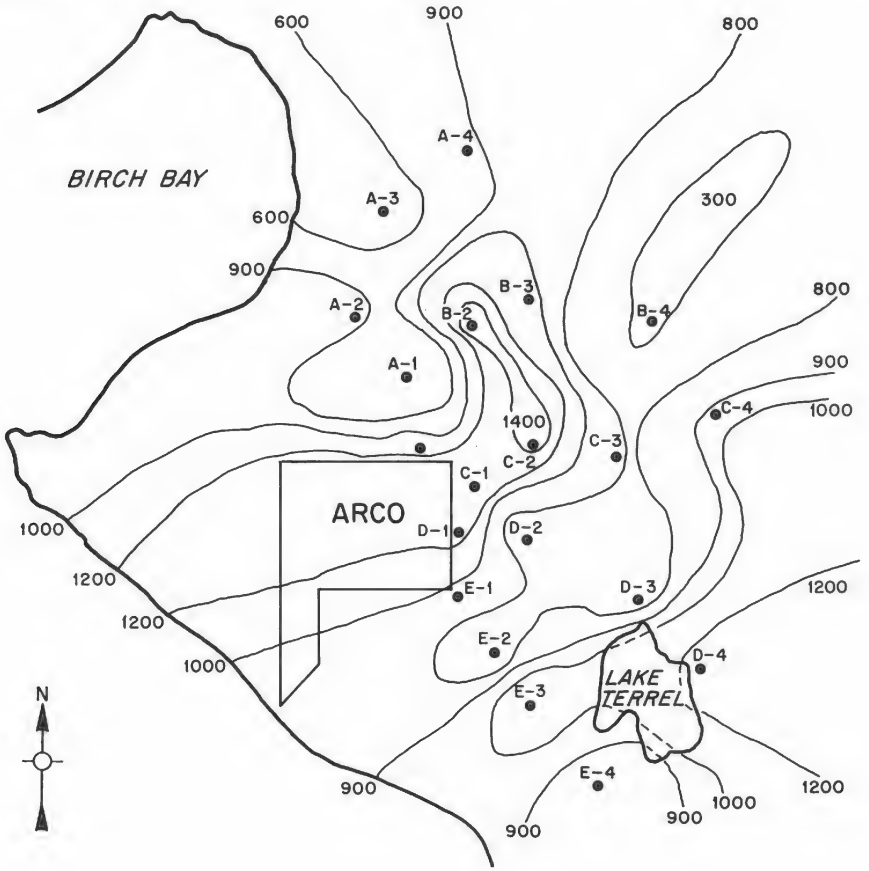


Figure 7. Isopleth showing the patterns of sulfur concentration (ppm) in alder leaves. Sampling sites are identified (see Fig. 1).

General Discussion

Results of this study and observations made by Taylor (1978) show that the lichen flora is being affected in the ARCO area, both in terms of total coverage and elimination of sensitive species from critical locations. However, even though there was a significant correlation between distance from ARCO and lichen coverage, the situation in the area is made more complex by the close proximity of Mobil Oil and, especially, Intalco Aluminum Corp. The latter emits critical levels of SO_2 (Northwest Air Pollution

Authority, unpub. data) as well as hydrogen fluoride. A study by Perkins *et al.* (1980) showed that fluoride accumulation by corticolous lichens (those epiphytic on trees) was negatively correlated with distance from an aluminum reduction plant and that lichen damage and reduced abundance was due to F^-. Perkins *et al.* also showed that there was a significant ($p \leq .05$) increase in fluoride accumulation up to 8 km from the source. A radius of 8 km from Intalco would encompass the whole of the ARCO study area.

Given the combination of pollution sources in northwestern Whatcom County and mixture of HF and SO_2 pollutants in the atmosphere, it becomes difficult to relate pollution damage with a single source, e.g., ARCO, or with a single pollutant, e.g., SO_2. This is especially true since SO_2 and HF may produce a synergistic response in vegetation (Mandl *et al.* 1975). Therefore the establishment of acceptable emission levels must, in a practical sense, consider all pollution sources and chemicals. A problem of equal concern is the determination of criteria to be used in establishment of acceptable emission levels. Existing standards tend to be directed toward protection of vascular plants, especially those of commercial value, ignoring the extreme sensitivity of most epiphytic lichens. This study is a case in point, i.e., results indicate that SO_2 emitted primarily from ARCO (Azimuth A) and from a mix of industries, in combination with HF (Azimuth C, D, and E), has seriously depleted the lichen flora, even though emission levels have generally remained within acceptable limits based on standards set by the Environmental Protection Agency. The question then becomes, "Why protect lichens?" Lichens are bioindicators and by ensuring their survival, pollution damage done to other organisms and to the environment as a whole can be kept to a minimum. But, more important, lichens are a part of that ecosystem and serve many important roles such as nitrogen fixation. Also, lichens deserve protection for aesthetic reasons.

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Differences in Amphibian Populations in Logged and Old Growth Redwood Forest

Abstract

Surveys of amphibians were done on 8 plots (0.125 ha each), consisting of 4 paired comparisons (logged and unlogged) in or near the Redwood National Park, California. The number and percentage cover of perennial vegetation were greater on old growth plots than on logged sites. Amphibian populations had more individuals and greater biomass, and different species composition on the old growth sites than on logged plots. Abundance of amphibians was lower in the redwood forests that had been logged 6-14 years ago. This evidence suggests that logging has a long-term effect on resident herpetofaunas of redwood forests. Apparently, opening of the canopy favors a few species to the detriment of the majority of forest-dependent species.

Introduction

Advertisements in national magazines imply that productive, abundant wildlife populations inhabit logged lands and that successional stages contain better habitat conditions for wildlife than do mature (sometimes termed decadent) forests. These claims are simplistic because the complexity and variability of mature forest ecosystems or the important roles of nongame wildlife are not considered in these systems.

Hassinger *et al.* (1975) stated that the net worth of a clearcut to wildlife must be viewed as a balance of values, since processes detrimental to one species may be beneficial to another. Logging creates vegetational diversity (e.g., edges and openings) and thus is generally beneficial to game because it promotes increased growth of herbaceous and shrubby foods that many game species require (Teague 1968, Noble 1974, Umber and Harris 1974, Costa *et al.* 1976). But game may constitute only a small fraction of forest wildlife, especially in mature stands (Bury *et al.* 1980).

Logging may drastically change or adversely affect the habitats of many animal species. In western North America, for example, small mammal communities are altered by timber harvesting. Deer mice (*Peromyscus maniculatus*) generally increase in numbers after logging, whereas red-backed voles (*Clethrionomys californicus*), red squirrels (*Tamiasciurus hudsonicus*), and other forest-adapted species decrease (Gashwiler 1970, Wolff and Zasada 1975, Hooven and Black 1976, Sullivan 1980). One study revealed that even big game (deer, elk, and moose) declined during the first 5 years after logging and that the carrying capacity of the forest when measured 17 years after logging was lower than expected (Stelfox *et al.* 1976).

Several authors have suggested that clean logging (removal or burning of downed wood and understory vegetation) reduces the abundance of small mammals (Lovejoy 1975, Martell and Radvanyi 1977, Hansson 1978) and game (Stelfox *et al.* 1976) by decreasing the supply of cover available to them. Recent studies indicate that logging

variously affects different animal taxa and decreases many wildlife species (Umber and Harris 1974, Glowacinski and Järvinen 1975, Shepard 1975, White *et al.* 1975, Bunnell 1976, Ahlén 1976, Franzeb 1977, Webb *et al.* 1977, Kessler 1979, Luman and Neitro 1980, Meslow *et al.* 1981, Schoen *et al.* 1981).

Because of diverse habitat conditions and forest types, the response of wildlife to logging is difficult to predict. More comprehensive data about the effect of timber harvesting on specific types of forests and on the nongame animals in these ecosystems would be useful in designing forest management practices favorable to wildlife populations. This study is the first to examine the effect of clearcut logging on the herpetofauna of old growth redwood forests.

Description of Study Areas

Four study areas were established in or adjacent to the Redwoods National Park in northwestern California: (1) Hill Plot and (2) Valley Plot, both in North Fork drainage of Lost Man Creek (Sec. 13, T.11N, R.1E), 3.5 km E of Hwy. 101 (from the Prairie Creek Fish Hatchery), Humboldt County; (3) Bald Hills (Sec. 1, T.10N, R.1E), 4.3 km E of Orick, along the Bald Hills road, Humboldt County; and (4) Yurok Redwood Experimental Forest (Sec. 21, T.14N, R.1E), 1.3 km N of the Ranger Station, Del Norte County. All distances are direct line.

Each study area consisted of two sampling sites (old growth and clear-cut logged) that had similar steepness (percent slope), slope direction, and major vegetation types (Table 1). On the Hill and Valley Plots and Bald Hills, the total number of live trees plus natural stumps more than 1 m DBH (diameter at breast height) were comparable to the number of stumps (cut trees) on the logged site. The Experimental Forest was more variable. The old growth site had more large trees ($N = 12$) than the logged site had large stumps ($N = 5$). But these two areas were only 200 m apart and seemed to have similar plant composition, and the entire area was once a contiguous stand of redwood.

Old growth sites at Lost Man Creek and the Experimental Forest were predominantly redwood (*Sequoia sempervirens*) with a few scattered Douglas fir (*Pseudotsuga menziesii*) and Sitka spruce (*Picea sitchensis*). Lost Man Creek was harvested 6-7 years before this study and had no trees larger than 10 cm DBH on logged sites. Logging had occurred 15 years earlier in the Experimental Forest (an area dominated by redwood), and the site had regrown with a tangle of small red alder (*Alnus oregana*). At Bald Hills, both sites had originally contained redwoods mixed with a few tanbark oak (*Lithocarpus densiflora*) and western hemlock (*Tsuga heterophylla*), and many small Douglas fir. Logging at the Bald Hills site had occurred about 10 years before this study.

Methods and Materials

Each sampling site measured 25 x 50 m (0.125 ha). All trees larger than 10 cm DBH were individually measured. On 10 squares (1 x 1 m), arranged in 10 domino configuration at each site, I recorded the number of perennial plants present and visually estimated the percentage of surface area that they covered. The number and sizes of pieces of surface debris (branches, downed small trees, and logging litter) that could be turned over were counted on all sites except the Hill Plot. This characteristic repre-

TABLE 1. Site characteristics and trees (>10cm DBH) of 8 sampling plots (0.125 ha each). Trees or stumps over 1 m DBH are given in bold type.

Character		Lost Man Creek Hill Plot		Lost Man Creek Valley Plot		Experimental Forest		Bald Hills RNP	
		Old Growth	Logged	Old Growth	Logged	Old Growth	Logged	Old Growth	Logged
Slope Direction		NE	NE	NNE	ENE	ENE	E	NNW	NNW
Slope (%) Est.		20	20	15	25	15	20	5	10
Canopy (%) Est.		85	0	75	0	80	10	65	5
TREES:									
Sequoia	Live	32 **11**	—	23 **6**	—	13 **12**	14[m]	10 **7**	29[m]
	Stumps	1[s]	10 **8**	1[s] **1**[s]	9 **8**	—	7 **5**	0	7 **7**
Pseudotsuga	Live	—	—	1 **1**	—	—	3	51	—
	Stumps	1[s] **1**[s]	3 **3**	**1**[s]	1	—	—	3 **1**	2 **2**
Picea	Live	—	—	3 **2**	—	—	—	—	—
Tsuga	Live	—	—	—	—	—	—	3	—
Lithocarpus	Live	—	—	—	—	—	—	7	4
	Stumps	—	—	—	—	—	—	—	1
Alnus	Live	—	—	—	—	—	32	—	—
Total	Live	32 **11**	0	27 **9**	0	13 **12**	49	71 **7**	33
	Stumps	2 **1**	13 **11**	2 **1**	10 **8**	0	7 **5**	3 **1**	10 **9**

s=snag
m=mostly in clumps

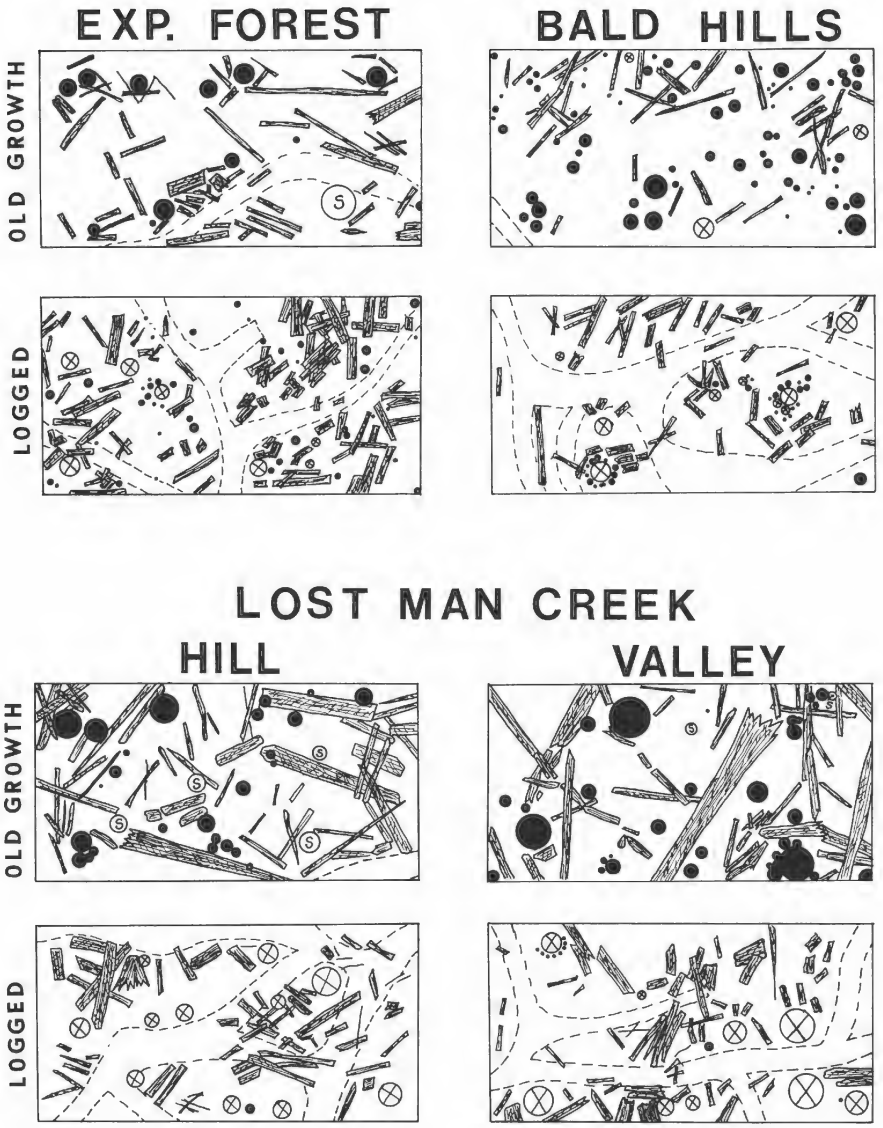

Figure 1. Trees and large downed wood of four paired plots (old growth and logged). Solid circles represent live trees; circles with an "X" are stumps and circles with an "S" are snags. Dashed lines depict logging (skid) roads. Each plot is 25 x 50 m.

sents the amount of small cover available to animals at each site. Larger debris that could not be moved (Fig. 1) also provided important cover.

Thorough searches for amphibians were conducted on each site by turning surface debris and small logs (less than 0.5 m diameter), and by raking through leaf litter. A team of two to five people worked each site and examined paired plots consecutively in order to minimize differences due to weather conditions. Field work was done from mid-January to early February 1975.

Animals were weighed to the nearest 0.1 g on field spring scales. Representative series were preserved as vouchers, and these specimens are deposited at the National Museum of Natural History, Washington, D.C.

Significance levels were $P<0.05$, unless otherwise stated.

Comparison of Vegetation and Cover

In general, old growth areas had more ferns, huckleberry, and salal than logged sites on which small conifers and alders predominated (Table 2.) The average number and percent cover of perennial plants on old growth sites was 40.2 (31-51) and 60.1 percent (32.5 -75.0 percent), respectively, which was greater than the average values of 30.0 (22-51) and 31.5 percent (20.0-52.5 percent) on logged sites. There were significantly more perennials at two old growth sites (Hill Plot, Bald Hills) and the logged area at the Experimental Forest (because of more small conifers and alders) than on their paired plots, but no difference at Lost Man Creek-Valley (χ^2 test). Percent cover was significantly greater on the unlogged than logged plots, except at Bald Hills (Test of Percentages).

Two of the old growth sites had significantly more surface debris than their logged counterparts (χ^2 test), but one logged site (Valley Plot) had almost the same amount of debris as the old growth site (Table 3). The percent of litter smaller than 0.6 m long was greater on logged sites ($\bar{x} = 66.8$ percent; range 61-73 percent) than on old growth sites ($\bar{x} = 48.0$ percent; range 44-52 percent). The large number of short pieces of litter on logged sites is partially produced by breakage of branches and trees during logging operations.

Differences in Amphibian Populations

Numbers of species and individuals, and the biomass of amphibians differed between old growth and logged sites (Table 4). The old growth sites had slightly more species ($\bar{x} = 3.5$; range 3-6) than did logged areas ($\bar{x} = 3.3$; range 2-4). This difference was not statistically significant, but there were distinct qualitative differences since certain species were found either in old growth or only on logged sites. The Olympic salamander (*Rhyacotriton olympicus*) and tailed frog (*Ascaphus truei*) occurred only in a rivulet through the old growth Hill Plot (Lost Man Creek), whereas the Pacific treefrog (*Hyla regilla*) was found only in a logged plot. Search of a rivulet in the logged area yielded no *Ascaphus* nor *Rhyacotriton*. Pacific giant salamanders (*Dicamptodon ensatus*) occurred on half of the old growth sites, but none were found in logged areas.

For each paired comparison, there were more individuals and greater biomass in old growth plots than in logged sites ($P< 0.01$, χ^2 test). Further, the relative abundance of species in old growth and logged sites was noticeably different (Table 4). There were more individuals of *Ensatina eschscholtzi* in old growth area ($N = 52$; $\bar{x} = 13$, range 4-22) than in logged sites ($N = 20$; $\bar{x} = 5$, range 3-8), and more *Batrachoseps attenuatus* in old growth ($N = 136$; $\bar{x} = 34$, range 18-61) than in

TABLE 2. Perennial plants recorded at 10 stations (total area=10 m²).
Abbreviations: N=Total number of individuals; C(%)=Percent cover.

Plants	Lost Man Creek Hill Plot				Lost Man Creek Valley Plot				Experimental Forest				Bald Hills RNP			
	Old Growth		Logged		Old Growth		Logged		Old Growth		Logged		Old Growth		Logged	
	N	C(%)	N	C(%)	N	C(%)	N	C(%)	N	C(%)	N	C(%)	N	C(%)	N	C(%)
Ferns (mostly **Polystichum**)	24	40.5	7	4.5	31	60.5	2	1.0	23	60.5	13	12.5	3	1.5	3	2.5
Huckleberry (**Vaccinium ovatum**)	10	12.0	—	—	3	8.5	1	0.5	5	6.0	9	11.5	11	12.0	1	1.0
Blackberry (**Rubus vitifolius**)	—	—	3	2.0	—	—	—	—	—	—	—	—	—	—	4	2.5
Thimbleberry (**Rubus parviflorus**)	—	—	—	—	—	—	—	—	—	—	5	4.5	—	—	—	—
Salmon Berry (**Rubus spectabilis**)	—	—	—	—	—	—	—	—	1	1.0	1	1.0	—	—	—	—
Salal (**Gaultheria shallon**)	8	7.0	—	—	2	4.0	2	2.5	2	7.5	1	0.5	7	3.5	1	1.0
Rhododendron (**Rhododendron macrophyllum**)	—	—	—	—	—	—	—	—	—	—	—	—	9	6.0	—	—
California Lilac (**Ceanothus** sp.)	—	—	1	5.0	—	—	6	15.5	—	—	17	20.0	—	—	—	—
Small Conifers (**Sequoia, Pseudotsuga**)	—	—	14	10.0	1	0.5	11	11.0	—	—	—	—	17	6.5	13	13.0
Small Alders (**Alnus oregana**)	—	—	—	—	—	—	—	—	—	—	5	2.5	—	—	—	—
Small Tan Bark Oak (**Lithocarpus densiflora**)	—	—	—	—	—	—	—	—	—	—	—	—	4	3.0	—	—
Totals	42	59.5	25	21.5	37	73.5	22	30.5	31	75.0	51	52.5	51	32.5	22	20.0

TABLE 3. Comparison of surface debris at 6 sampling plots.

LOST MAN CREEK—VALLEY PLOT

Length (m)	OLD GROWTH Diameter (cm) <30 <10	<30 10-19	<30 20-19	30-59	60-119	>120	TOTALS (%)	LOGGED Diameter (cm) <30 <10	<30 10-19	<30 20-29	30-59	60-119	>120	TOTALS (%)
<0.6	242	80	22	2	0	0	345 (43.6)	360	111	58	5	0	0	534 (67.1)
0.6-1.2	168	30	10	2	0	0	210 (26.5)	90	47	27	9	2	0	175 (22.0)
1.2-1.8	114	18	6	0	3	0	141 (17.8)	34	13	5	2	3	0	57 (7.2)
1.8-2.4	50	3	1	1	0	0	55 (6.9)	9	10	1	1	0	0	21 (2.6)
2.4-3.0	19	1	4	1	0	0	25 (3.2)	0	1	2	1	0	0	4 (0.5)
>3.0	9	2	3	2	0	0	16 (2.0)	1	2	2	0	0	0	5 (0.6)
TOTALS (%)	602 (75.9)	134 (16.9)	46 (5.8)	8 (1.0)	3 (0.4)	0	793	494 (62.1)	184 (23.1)	95 (11.9)	18 (2.3)	5 (0.6)	0	796

EXPERIMENTAL FOREST

Length (m)	OLD GROWTH Diameter (cm) <30 <10	<30 10-19	<30 20-19	30-59	60-119	>120	TOTALS (%)	LOGGED Diameter (cm) <30 <10	<30 10-19	<30 20-29	30-59	60-119	>120	TOTALS (%)
<0.6	483	109	62	8	0	0	662 (51.9)	395	101	34	2	0	0	532 (72.7)
0.6-1.2	283	56	45	7	1	0	392 (30.8)	63	35	28	3	0	0	129 (17.6)
1.2-1.8	89	37	14	5	0	1	146 (11.5)	5	20	14	4	4	0	47 (6.4)
1.8-2.4	23	13	10	3	1	0	50 (3.9)	2	4	4	3	0	0	13 (1.8)
2.4-3.0	10	4	3	1	0	0	18 (1.4)	0	1	0	1	0	0	2 (0.3)
>3.0	2	2	1	2	0	0	7 (0.5)	0	2	3	1	3	0	9 (1.2)
TOTALS (%)	890 (69.8)	221 (17.3)	135 (10.6)	26 (2.0)	2 (0.2)	1 (0.1)	1275	465 (63.5)	163 (22.3)	83 (11.3)	14 (1.9)	7 (1.0)	0	732

TABLE 3. continued

BALD HILLS—RNP

Length (m)	OLD GROWTH Diameter (cm) <30 <10	<30 10-19	<30 20-29	30-59	60-119	>120	TOTALS (%)	LOGGED Diameter (cm) <30 <10	<30 10-19	<30 20-29	30-59	60-119	>120	TOTALS (%)
<0.6	404	53	15	1	0	0	473 (52.5)	283	77	29	3	0	0	392 (60.7)
0.6-1.2	207	15	6	3	0	0	231 (25.7)	83	33	15	11	1	0	143 (22.1)
1.2-1.8	106	10	3	2	0	0	121 (13.4)	44	17	7	2	0	0	70 (10.8)
1.8-2.4	29	3	2	0	0	0	34 (3.8)	11	6	4	1	0	0	22 (3.4)
2.4-3.0	22	0	0	0	0	0	22 (2.4)	7	3	3	1	0	0	14 (2.2)
>3.0	15	2	2	1	0	0	20 (2.2)	3	0	1	1	0	0	5 (0.8)
TOTALS (%)	783 (86.9)	83 (9.2)	28 (3.1)	7 (0.8)	0	0	901	431 (66.7)	136 (21.1)	59 (9.1)	19 (2.9)	1 (0.2)	0	646

logged sites (N = 21; $\bar{x}$ = 3.3, range 1-9). *Aneides ferreus* was more abundant in logged areas (N = 35; $\bar{x}$ = 8.8, range 0-30) than in old growth (N = 12; $\bar{x}$ = 4, range 0-9). This species constituted 68 percent of the herpetofauna at the Bald Hills logged area.

Sampling of quadrats required intensive search effort and relatively few animals were found per person-hour (Table 4). More time was required to sample old growth plots due to the greater amount of leaf litter present there than in logged areas.

Discussion

This study indicates that there is a distinct change in the species composition of both the perennial plants and the amphibians following logging of redwood forests. Relative abundances of animals also differ in old growth and post-logging habitats.

Logging opens the forest canopy and apparently favors only a few species of amphibians to the detriment of the majority— the forest-dependent species. The salamanders *Ensatina* and *Batrachoseps* were found principally in old growth redwood stands, in agreement with results of an earlier study at a locality about 100 km farther south (Bury and Martin 1973). Also, *Aneides ferreus* at this southern area was more prevalent in second-growth than in primary forests, the pattern that held in the present study. Because this species frequents crevices and bark under downed timber in California (Stebbins 1951, Bury and Martin 1973), logging apparently provides its preferred habitat conditions. Old growth sites examined in the present study had several species (*Ascaphus*, *Rhyacotriton*, and *Dicamptodon*) that were absent on logged areas. *Ascaphus* and *Rhyacotriton* frequent cold, flowing waters (Bury 1968, Stebbins 1966), whereas *Dicamptodon* usually occurs in forested environs.

Amphibians were more abundant in old growth forests than in logged areas. Similarly, in South Carolina, Bennett *et al.* (1980) found a higher number of amphibians in natural oak-hickory habitat than in nearby managed pine habitats.

I suggest a scenario of events that resulted in these changes of amphibians. Clearcut logging opens the redwood forest canopy. The increased light penetration on the forest floor leads to increased soil temperatures and, in turn, greater evaporative water loss from the soil and understory. Opened areas also are subject to greater daily fluctuations in temperature and humidity than in primary forests.

Barren soil occurs in parts of logged areas, apparently a result of increased microbial activity (related to higher ambient temperatures) combined with erosion of the organic top soil and humus, which occurs rapidly in a region receiving about 180 cm of precipitation each year. Also, logged areas lack nutrients through leaf fall from large trees. These conditions reduce leaf litter as a microhabitat for amphibians.

Available cover for amphibians in both old growth and logged redwood forests was ample (Table 3), particularly since these counts did not include immovable fallen trees, buried debris, and stumps (Fig. 1). Also, leaf litter (which was not measured) provided refuge for animals in old growth forests.

Although two of the three old growth sites contained greater amounts of cover, logged plots also had large numbers of cover items. The difference in cover supply apparently was not responsible for the differences in terrestrial vertebrates occurring in native or harvested redwood forests. Rather, microclimatic, vegetational and other

TABLE 4. Herpetofauna taken on 8 sampling plots (0.125 ha each). Weight (Wt) is in grams.

Species		Lost Man Creek Hill Plot				Lost Man Creek Valley Plot				Experimental Forest				Bald Hills RNP			
		Old Growth		Logged		Old Growth		Logged		Old Growth		Logged		Old Growth		Logged	
		N	Wt	N	Wt	N	Wt	N	Wt	N	Wt	N	Wt	N	Wt	N	Wt
Ensatina eschscholtzi		4	6.5	5	12.8	8	15.3	3	7.7	18	39.4	8	18.1	22	55.0	4	8.5
Aneides ferreus		—	—	—	—	1	1.4	—	—	9	20.9	5	13.2	2	3.2	30	67.5
Batrachoseps attenuatus		18	11.5	1	0.3	20	13.1	2	1.8	61	34.8	9	6.0	37	27.3	9	7.4
Ambystoma gracile		—	—	—	—	—	—	—	—	—	—	2	31.2	—	—	—	—
Dicamptodon ensatus	larvae	3	2.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	juvenile	1	28.0	—	—	—	—	—	—	—	—	—	—	2	88.8	—	—
Rhyacotriton olympicus	larvae	2	0.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Plethodon elongatus		—	—	—	—	—	—	—	—	—	—	—	—	1	3.8	—	—
Ascaphus truei		1	6.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hyla regilla		—	—	1	0.3	—	—	—	—	—	—	—	—	—	—	—	—
Total		29	55.7	7	13.4	29	29.8	5	9.5	88	95.1	24	68.5	64	178.1	43	83.4
Person-hours		19.5		7.5		36.0		7.5		44		16.5		31.5		9	
N/person-hr		1.5		0.9		0.8		0.7		2.0		1.5		2.0		4.8	

changes that occur after logging apparently result in unsuitable conditions for many amphibians.

The resident, forest-dependent amphibians are drastically altered in both species composition and abundance after logging. Amphibians had not recovered on sites sampled 6-14 years after logging. It is not known how long a logged area requires to revert naturally to a condition in which the fauna typical of old growth redwood is regained. Further, it is not known what can be done to expedite the recovery of these wildlife communities after timber harvesting.

Amphibians are often neglected in studies of ecosystems, but they are important. For example, Burton and Likens (1975) demonstrated that salamanders in a forest ecosystem may comprise a biomass twice that of birds and equal to mammals. Amphibians may be equally important to redwood forests. In old growth stands, I found 420 amphibians per ha, and I believe that this figure probably underestimated the resident populations, since my sampling was conducted during a time of cool to freezing temperatures and low rainfall, conditions that are not favorable for surface activity by amphibians.

Recently, the Redwood National Park acquired logged land adjacent to the park as buffer zones. These areas had been logged by clearcutting with little or no regard for the unique wildlife communities associated with the old growth redwood. Large block cuts left no shade or islands of natural forest (to provide reservoirs for reinvasion), and the terrain is scarred and strewn with logging debris.

Because national and state redwood parks are managed for aesthetic and biotic values, we face a challenge in the rehabilitation of logged redwood forests that have been acquired as buffer zones for parks. The present study suggests that logging has a long term detrimental effect on most species of amphibians in the redwood region, and that the addition of cover or the piling of debris in logged redwood areas would probably not promote the recovery of amphibians. Although amphibians are the most abundant vertebrate of redwood forests, we cannot manage their populations because we lack knowledge of the unique fauna of old growth redwood forests; we also do not understand how logged wasteland can be restored to suitable habitat for forest-dependent wildlife.

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Correlation of Late Cenozoic Gravel Deposits along the Yakima River Drainage from Ellensburg to Richland, Washington

Abstract

Gravel deposits are sampled for clast lithology at fifty-seven sites along the Yakima River from Thorp to Richland, Washington. One hundred clasts, in each of three different sizes, are identified from each site. These are divided into five lithologic groups: basalt, andesite, granitic, metamorphic, and sedimentary. Gravels from the modern Yakima River, three Yakima River terraces, the Ellensburg Formation, and the Ancestral Columbia River are compared.

The modern Yakima River is influenced by four downstream sediment sources: detritus from the Naches River, gravel deposited by the ancestral Columbia River, landslide deposits, and gravel related to the Spokane Flood.

The percentage of pink and gray rhyodacite clasts derived from the Ellensburg Formation can be used effectively to separate Yakima River terrace gravels, Thorp gravels, and Ellensburg Formation gravels. Weathering rinds on basalts are helpful in determining the relative ages of gravel deposits.

The Lakedale and Thorp terrace levels present in the upper Kittitas Valley can be traced downstream as far as Toppenish, Washington, but flood deposits and landslide debris mask terrace outcrops downstream from Toppenish.

Introduction

The Yakima River, located in southcentral Washington, is a major tributary to the Columbia River (Fig. 1). The Yakima River drains portions of the Cascade Range and the portion of the Columbia Basin geologic province containing the Yakima fold belt. Field studies conducted from 1978 to 1980 along the Yakima River drainage and its tributaries from Ellensburg to Richland, Washington, revealed many gravel deposits and terrace remnants. Numerous investigators describe gravels within the Yakima River drainage. Rigby and Othberg (1979), and Meyer and Price (1980) give excellent summaries of previous studies done on gravel deposits lying above the youngest basalt flows. Waitt (1979) has done the most detailed work on gravel deposits in the Kittitas Valley. Fission track dating of tephras and geomorphic evidence documents Waitt's work on the Thorp Gravel and other younger terrace deposits. However, his work is restricted to the upper Kittitas Valley north of Ellensburg, Washington, and to gravels younger than Thorp. Other workers have mapped or described in detail portions of the gravels, and some have combined several distinct gravel units as one. These methods have resulted in confusion and miscorrelation of many gravel deposits.

This study describes and correlates various gravel units on the basis of lithology, weathering, and geomorphic evidence, beginning at Ellensburg (Waitt's southern boundary) and continuing downstream to Richland.

Rock Units

Gravel samples for this study were collected from the following units: modern Yakima alluvium, Yakima terrace gravels, terrace gravels thought to be Thorp equivalent, Ellensburg Formation, and gravels related to the ancestral Columbia River. Figure 2 shows the locations of each gravel sample site.

Modern gravels were collected from the Yakima River (Thorp to Richland) to identify lithologies that could occur and to provide a control for identifying older gravels. Additional samples were collected along the lower Naches, Tieton, and Toppenish tributaries to determine their influence on the Yakima River.

As many as three terrace gravel deposits occur along the Yakima River as far south as Toppenish. A lower terrace with an elevation of 5 m above the modern Yakima

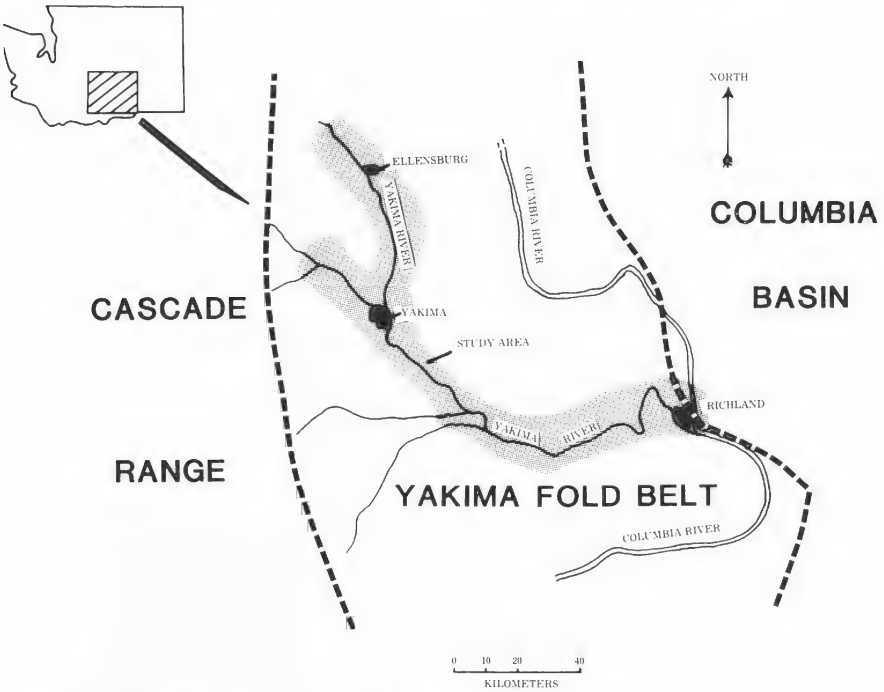

Figure 1. Location map showing the study area.

River flood plain is present in the lower Kittitas Valley, at Yakima, and between Wapato and Toppenish. A second, middle terrace is present in the lower Kittitas Valley, in isolated remnants in the Yakima River Canyon, at Yakima, and between Wapato and Toppenish. The middle terrace is at an elevation of 10 m (9-18 m range) above the modern Yakima flood plain and corresponds in position to Waitt's (1979) Lakedale drift.

A third, upper terrace, known in the Kittitas Valley as the Thorp Gravel, exists along the Yakima River from the Kittitas Valley to Toppenish. Gravel deposits occur-

ring at similar elevations around Yakima are informally called Thorp by Campbell and Bentley (Meyer and Price 1980, Bentley *et al.* 1980). Gravels corresponding in elevation to the Thorp Gravel are found in isolated patches and terrace remnants in the Yakima River Canyon, at Yakima, and near Wapato. The elevations of these gravels are approximately 60 m (20-100 m range) above the modern flood plain.

Waitt (1979) divides terrace gravels in the upper Kittitas Valley into a mainstream (mixed lithologies) and a sidestream (basalt dominant) facies. Only mainstream gravels are sampled in this study, but terrace gravels corresponding to a sidestream facies crop out along small tributaries downstream from the Kittitas Valley throughout the study area.

Gravels collected from the Ellensburg Formation include those from the Kittitas Valley, lower Naches River (type section), around Yakima, and in the Toppenish-

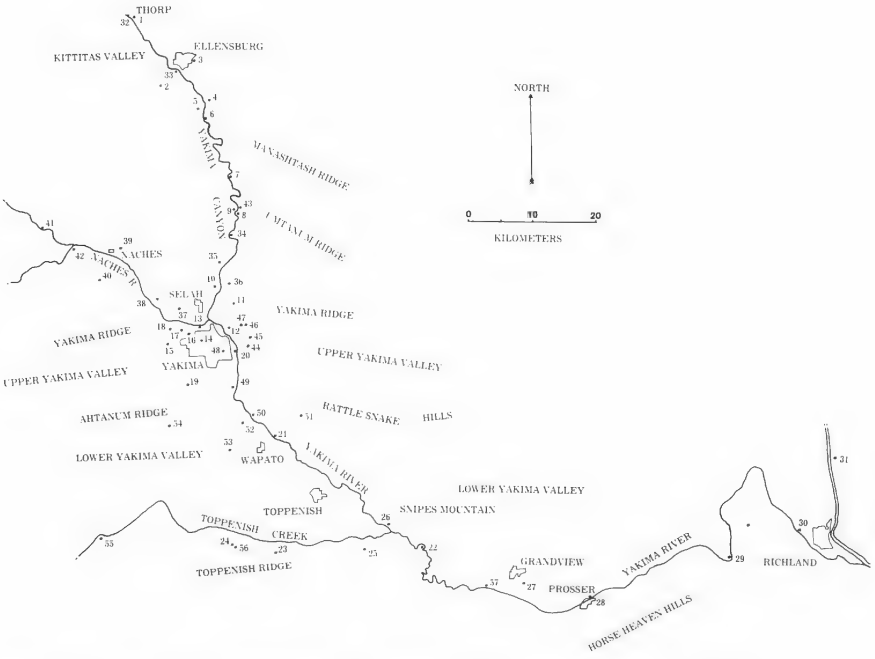

Figure 2. Location map showing gravel collection sites in the Yakima River drainage.

Wapato area. These gravels are found at a wide range of elevations, are often in steeply dipping beds, and are not related to the present Yakima or Naches drainage systems.

Gravels related to the ancestral Columbia River (also known as the Hood River and Snipes Mountain Conglomerates), the Spokane flood, and the middle Ringold Formation were also sampled from widely scattered locations in order to determine their influence on the lower Yakima River from Wapato to Richland (Fig. 2).

Sampling Methods

The fifty-seven sites between Thorp and Richland are distributed as follows:

Modern Yakima River alluvium	11 sites
Yakima River tributaries	4 sites
Lower Yakima River terrace	2 sites
Middle Yakima River terrace	7 sites
Upper Yakima River terrace (Thorp equivalent or at elevations corresponding to Thorp Gravel)	10 sites
Gravels that are part of the Ellensburg Formation	13 sites
Ancestral Columbia River Gravels	3 sites
Miscellaneous gravel	7 sites

Three hundred clasts were sampled from each site. One hundred clasts were collected in each of three size ranges: 1-3 cm, 4-6 cm, and 8-25 cm. In order to ensure a relatively unbiased sample, a steel tape was stretched at random across the outcrop and clasts were collected along the tape. This method of collection could not be used at sites with overhanging ledges. At these sites an alternate method, picking a random spot and collecting outward in all directions, was used. At each site, the 1-3 cm and 4-6 cm fractions were sacked for counting in the lab. The 8-25 cm fraction was split and counted at the site; selected clasts were collected that showed weathering rinds and characteristic lithologies. The 1-3 cm and 4-6 cm clasts were cracked and counted in the lab. All samples were counted under the same lighting conditions for consistency.

The clasts are divided into five rock groups: basalt, andesite, granitic, metamorphic, and sedimentary. Almost all basalt clasts are derived from the Yakima Basalt subgroup. The andesite group includes a wide variety of andesite, dacite, volcanic breccia, and pink to grey rhyodacites. Included with the granitics are all coarse-grained igneous rocks and coarse metamorphics such as gneiss. Clasts included with the metamorphics are quartzite, schist, other fine-grained metamorphic rocks, chert, and vein quartz. Sedimentary clasts include sandstone, shale, graywacke, and conglomerate.

One problem encountered during the counting process involved the difficulty in correctly identifying weathered clasts in older gravels. Highly weathered and bleached basalt can closely resemble sedimentary clasts. Some weathered andesites and granitics, when crumbly, are difficult to distinguish. However, in the most highly weathered samples, there were usually no more than 3 percent questionable clasts. Several of these sites were re-sampled and re-counted to test for variations in accuracy. The re-counted samples fall within the 3 percent error of the original samples.

Figures 3 through 9 show the results of the pebble counts. The composition percentages for all five rock groups (three sizes plus an average) are plotted for each site. The percentage of pink and gray rhyodacites is tabulated for each site, as these were found to be important in distinguishing some older gravels.

The graphs clearly show that, with few exceptions, there is little difference in composition between sizes, especially the two smaller fractions. The 8-25 cm fraction tends to have slightly more granitics and fewer basalt clasts than the finer fractions. The results show that gravels along the Yakima River drainage maintain the same composition regardless of size.

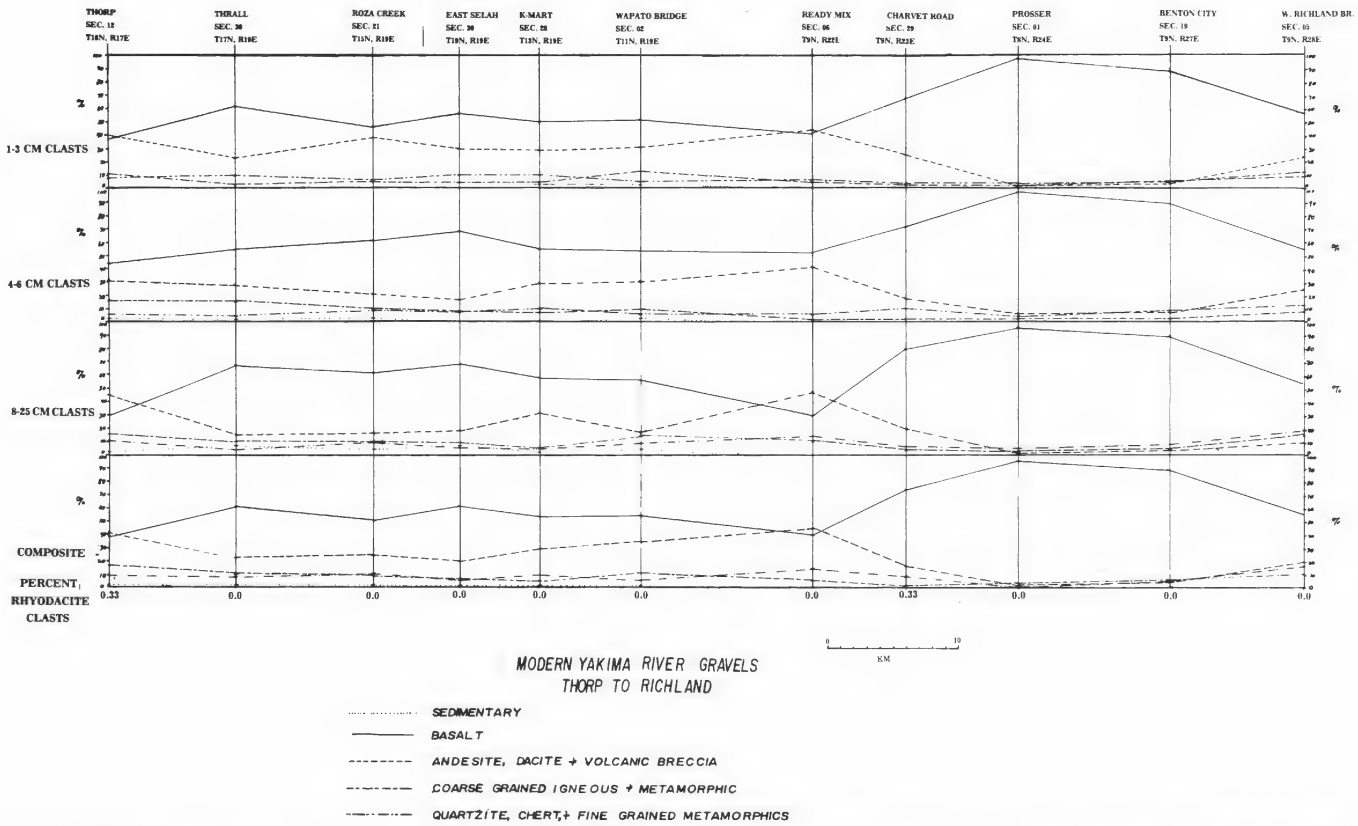
THORP SEC. 12 T18N, R17E
THRALL SEC. 30 T17N, R18E
ROZA CREEK SEC. 21 T15N, R19E
EAST SELAH SEC. 30 T18N, R19E
K-MART SEC. 28 T15N, R19E
WAPATO BRIDGE SEC. 02 T11N, R19E
READY MIX SEC. 06 T9N, R22E
CHARVET ROAD SEC. 29 T8N, R23E
PROSSER SEC. 01 T8N, R24E
BENTON CITY SEC. 19 T8N, R27E
W. RICHLAND BR. SEC. 05 T8N, R28E
1-3 CM CLASTS
4-6 CM CLASTS
8-25 CM CLASTS
COMPOSITE
PERCENT RHYODACITE CLASTS
0.33 0.0 0.0 0.0 0.0 0.0 0.0 0.33 0.0 0.0 0.0
0 10
KM
MODERN YAKIMA RIVER GRAVELS
THORP TO RICHLAND
SEDIMENTARY
BASALT
ANDESITE, DACITE + VOLCANIC BRECCIA
COARSE GRAINED IGNEOUS + METAMORPHIC
QUARTZITE, CHERT, + FINE GRAINED METAMORPHICS

Figure 3. Graph showing composition of gravels of the modern Yakima River. Three sizes and the composite of all sizes are shown for five separate rock groups. The rhyodacite percentage for each site is shown at the bottom of the graph.

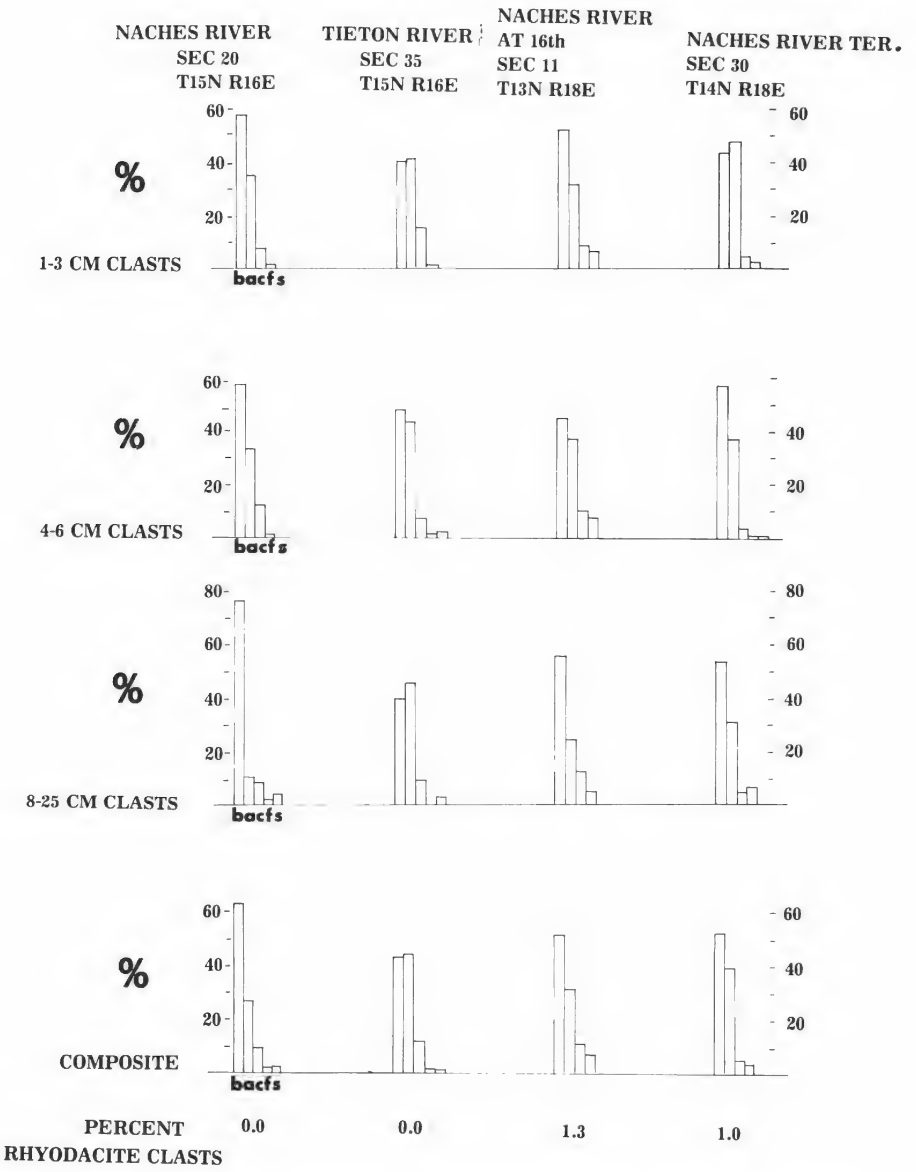

Figure 4. Graph showing the composition of gravels along the Naches-Tieton River drainage. Three sizes and the composite of all sizes are shown for five separate rock groups. The rhyodacite percentage for each site is shown at the bottom of the graph.

Lithology and Correlation

Modern River Gravels

Samples were taken along the Yakima River from Thorp to Richland, on the lower Naches and Tieton drainage, and on Toppenish Creek (Figs. 3 and 4). The gravels sampled were from bars that extend well into the river at low water. The composition of the gravel in the Yakima River is clearly influenced by downstream sources of sediment. The Naches River, Snipes Mountain, landslide debris, and Spokane Flood gravels all contribute to the Yakima River lithology.

The Yakima River passes close to, and is influenced by, Snipes Mountain, which is partially composed of ancestral Columbia River gravels. The very high percentage of basalt at Prosser is difficult to explain but may be the result of landslide debris coming off the Horseheaven Hills or from sediment received from Satus and Toppenish Creek (100 percent basalt clasts). Spokane Flood gravels also appear to influence the Yakima River downstream from Benton City.

The lower Naches River gravel is quite similar in composition to that of the Yakima River. In general, the Naches contains a few more green andesites, volcanic breccias and gneiss, but the differences in lithology are slight.

One important rock type not carried by the Yakima or Naches Rivers is pink to gray rhyodacites derived from lahars of the Ellensburg Formation. Although the Naches River flows past 10 km of thick, poorly cemented Ellensburg Formation containing lahars with a high percentage of rhyodacites, there are very few of these clasts (1.33 percent or less) in the modern alluvium. The Yakima contains less than 0.33 percent rhyodacite clasts. The percentage of these clasts is significant in distinguishing Yakima River and Thorp from Ellensburg gravels.

The shape of clasts collected from modern alluvium varies from round to subangular. Smaller clasts tend to be slightly rounder than larger-sized gravel. Basalts are usually more angular and metamorphics flatter than other clasts, but the variations in shape from one locality to another are slight.

Weathering of basalt creates weathering rinds that are easily visible in broken clasts. The thickness of the rinds observed in modern alluvium varies from zero for fresh basalt to 12 mm for weathered clasts. Most rinds range from 2 to 5 mm in thickness, with rinds present on less than 25 percent of all basalt. Granitics, metamorphics, and andesites show almost no weathering rinds in samples from the modern Yakima River.

Lower and Middle Yakima River Terraces

Terrace gravel deposits can be easily identified along the Yakima River as far downstream as Toppenish. A lower terrace, having an elevation of about 5 m above the modern Yakima River flood plain, is present in the lower Kittitas Valley, near Selah and Yakima, and between Wapato and Toppenish (Fig. 5). The lower terrace was sampled in only two locations because of the difficulty in finding good exposures. The lower terrace has been modified by irrigation, ditching, and farming. Weathering rinds are not common in basalts and, when present, average 2-5 mm in thickness. The exact age of the lower terrace is unknown, no caliche or other datable material having been found.

A second or middle terrace is present in the lower Kittitas Valley, in isolated remnants

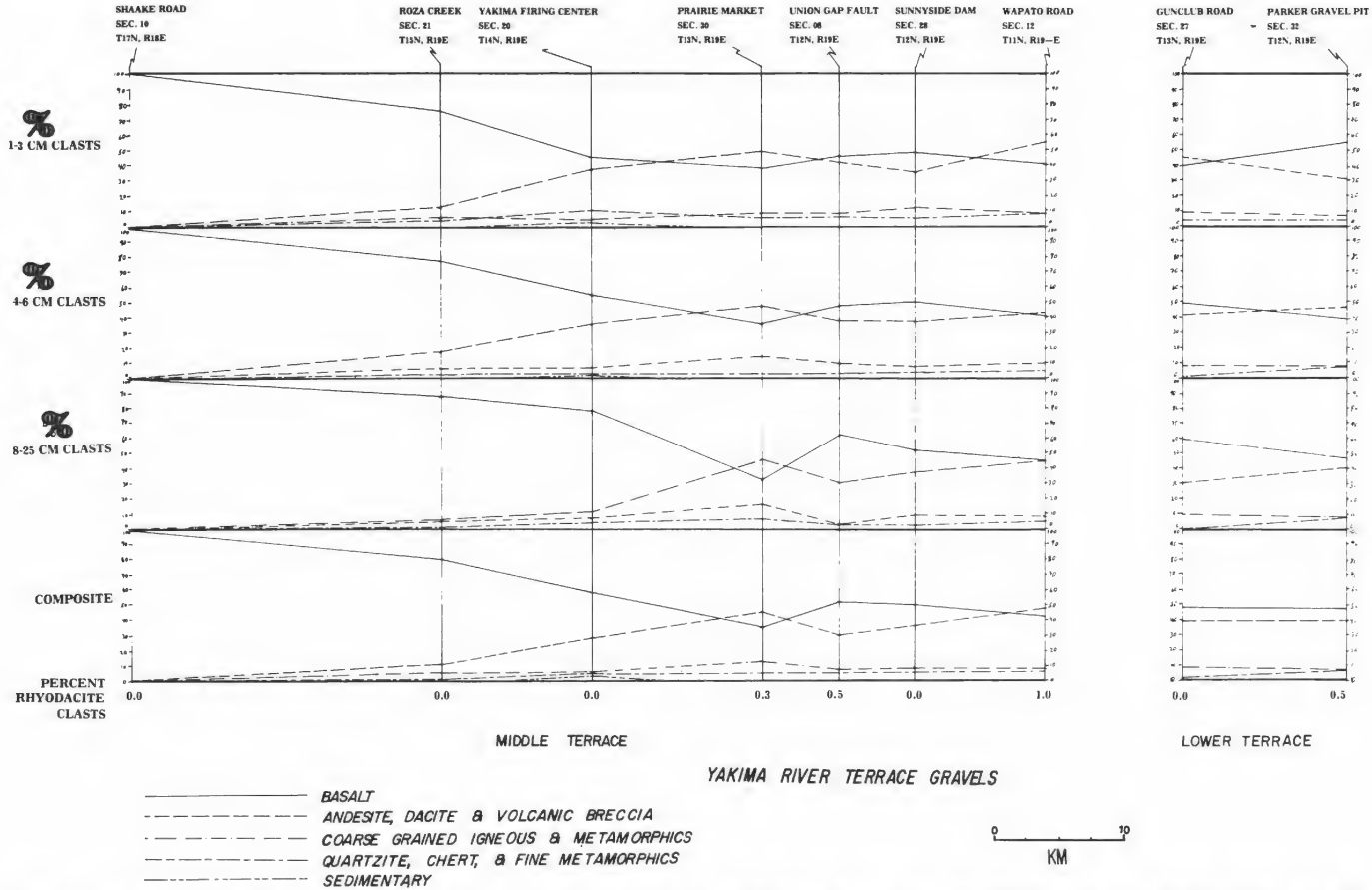

Figure 5. Graph showing the composition of the lower and middle Yakima River terraces. Three sizes and the composition of all sizes are shown for five separate rock groups. The rhyodacite percentage for each site is shown at the bottom of the graph.

in the Yakima Canyon, at Selah and Yakima, and between Wapato and Toppenish (Fig. 5). The middle terrace lies at an elevation of about 10 m (range 8-18 m) above the modern flood plain and corresponds in elevation and position to the Lakesdale Drift of Waitt (1979) in the Kittitas Valley.

The middle terrace shows an increase in andesite and a decrease in basalt downstream from Ellensburg, with a surge in andesite clasts below the Naches River confluence (Fig. 5). Terrace gravels of similar elevations extend upstream along the Naches River and along Wide Hollow Creek and Ahtanum Creek near Yakima. Naches terrace gravels are difficult to distinguish from Yakima terrace gravels because of similar composition; the terrace at Prairie Market could also have been deposited by the Naches River.

Basalts from the middle terrace show slightly more weathering. The middle terrace weathering rinds on basalts average 3-6 mm, with some as thick as 12 mm. Between 25-50 percent of the basalts have rinds, but the rest appear quite fresh. Andesites and metamorphics appear relatively fresh, but granitics are more weathered than those of the lower terrace and the modern Yakima River.

The percentage of pink and grey rhyodacites (0 to 0.5 percent) derived from the Ellensburg Formation is low for both terraces and distinguishes these deposits from older gravel along the Yakima River.

Touchet beds containing the St. Helen's "S" tephra (age 13,000 years BP) rest on the middle terrace in several places in the lower Yakima River Valley. The middle terrace can therefore be considered older than 13,000 years. A caliche horizon developed on the middle terrace (near Union Gap) has been dated by the U/Th method at approximately 30,000 years, $\pm$ 3000 years (Ku 1979, unpub. data).

The middle terrace has been traced downstream as far as Toppenish. Loess, landslide debris, and Spokane Flood deposits obscure the terrace and prevent it from being traced into the Pasco Basin.

Upper Terrace (Thorp and Thorp-like Gravels)

A third or upper terrace exists along the Yakima River from the Kittitas Valley downriver as far as Toppenish. The sediments making up this terrace level are known as the Thorp Gravel in the Kittitas Valley (Waitt 1979). Gravels occurring at similar elevations in the Yakima area have been informally called Thorp (Rigby and Othberg 1979). Gravels corresponding in elevation to the Thorp gravel occur in isolated patches and outcrops in the Yakima Canyon, at Selah and Yakima, and near Toppenish. The elevations of the upper terrace gravels are approximately 60 m (range 20-100 m) above the flood plain. The elevations vary more than the lower and middle terraces because much of the original terrace has been removed by erosion. Only mainstream gravels were sampled, but gravels containing 100 percent basalt (sidestream facies) can be found along several tributaries in the Yakima Valley.

There is a decrease in basalt and increase in andesite southward from the mouth of the Yakima River Canyon (Fig. 6). More granitics usually occur in the coarse fraction (8-25 cm), and the percentage of pink and grew rhyodacites is low (0 to 2.6 percent). Two exceptions are the East Selah fault site (9.6 percent) and the Nightengale Road site (10.0 percent), where the values correspond more closely to gravels of the Ellensburg Formation (Fig. 7). Although the elevation of these two outcrops cor-

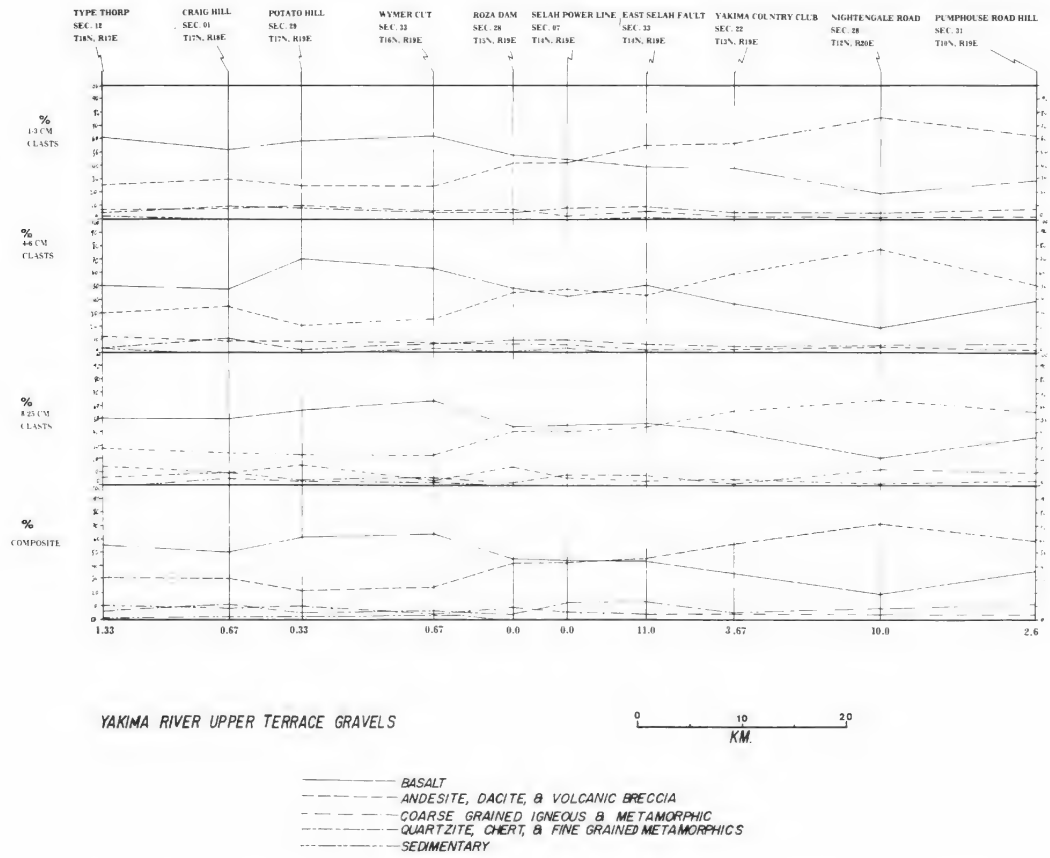

Figure 6. Graph showing the composition of the upper Yakima River terrace (Thorp Gravel). Three sizes and the composition of all sizes are shown for five separate rock groups. The rhyodacite percentage for each site is shown at the bottom of the graph.

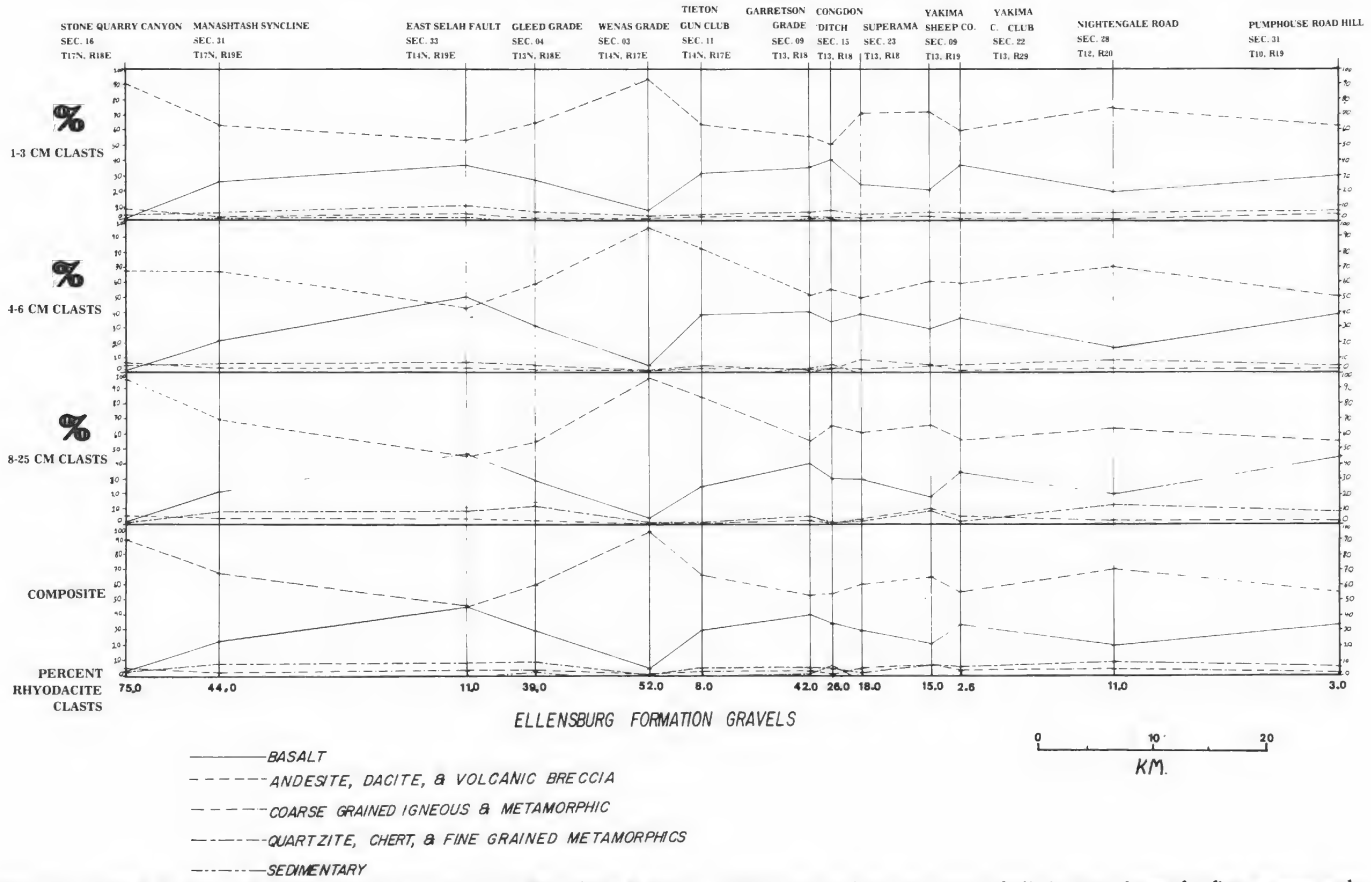

Figure 7. Graph showing the composition of gravels in the Ellensburg Formation. Three sizes and the composite of all sizes are shown for five separate rock groups. The rhyodacite percentage for each site is shown at the bottom of the graph.

respond to that of other Thorp Gravel sites, their composition suggests that they are part of the Ellensburg Formation.

Thick weathering rinds are developed on basalt clasts and average 5 to 7 mm, with a maximum thickness of 15 mm. More than 50 percent of all basalts have rinds developed, and many have bleached centers. Andesites display weathering rinds as much as 3 mm thick. Some brown andesites are quite crumbly, and granitics tend to be highly weathered and friable. Based on weathering characteristics, the gravels of the upper terrace appear to be significantly older than the middle terrace.

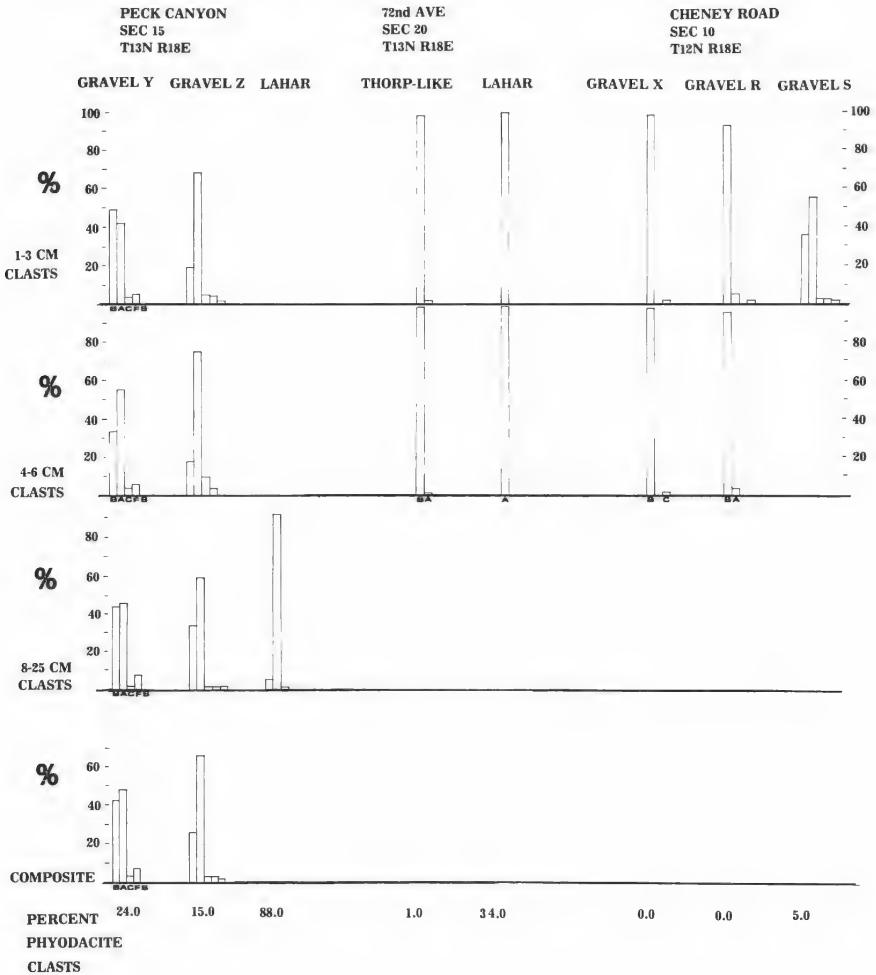

Figure 8. Graph showing the composition of mixed-layer gravel sites in the Ellensburg Formation. Three sizes and the composite of all sizes are shown for five separate rock groups. From left to right: B, basalt; A, andesite, dacite, and volcanic breccia; C, coarse-grained igneous and metamorphic; F, quartzite, chert, and fine-grained metamorphics; S, sedimentary.

Gravels of the Ellensburg Formation

Gravels from the Ellensburg Formation were sampled in the Kittitas Valley, along the lower Naches River, near Yakima, and in the Wapato-Toppenish area. Figure 7 shows the location and composition of the gravel sites. In general, the percentage of basalt increases downstream along both the Yakima and Naches Rivers. The percentage of pink or grey rhyodacites is significant and ranges from 11-75 percent, compared to less than 2.6 percent for Thorp Gravel. The high percentage of these clasts gives a clear distinction between Thorp and Ellensburg gravels.

Gravels of the Ellensburg Formation are more intensely weathered than those of

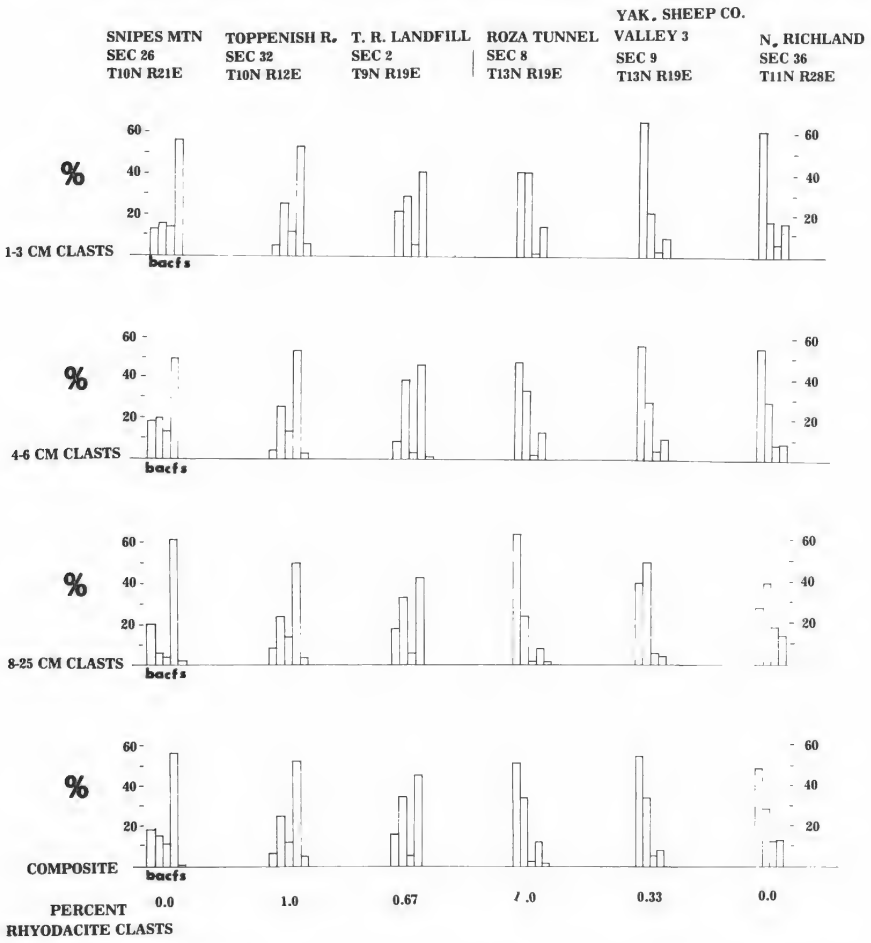

Figure 9. Graph comparing the composition of gravels of the ancestral Columbia River in the lower Yakima Valley (Snipes Mtn., Toppenish Ridge, and T. R. Landfill) with two upper valley locations (Roza Tunnel and Yakima Sheep Co.) and the middle Ringold Formation (N. Richland). Three sizes and the composite of all sizes are shown for five separate rock groups. The rhyodacite percentage for each site is shown at the bottom of the graph.

the Thorp. Basalts are often highly bleached and crumbly, with weathering rinds of as much as 15 mm in thickness. Andesites often show weathering rinds to 6 mm in thickness. Granitics are usually highly weathered and crumbly. However, weathering characteristics alone are not sufficient to distinguish Thorp and Ellensburg gravels.

The upper part of the Ellensburg often contains intermixed basalt-rich and rhyodacite-rich gravel layers, making the contact between the top of the Ellensburg Formation and base of the Thorp Gravel difficult to determine. Many of the best exposures of the Ellensburg Formation contain such interbedded gravels (Fig. 8). The basalt-rich layers can easily be confused with Thorp mainstream or sidestream gravels. As previously described, the basalt gravels in the Ellensburg Formation often contain a much higher percentage of rhyodacite clasts and thus can be distinguished from Thorp Gravel by lithology. However, there are exceptions. For example, the gravel at Gleed Glade contains only 3 percent rhyodacite clasts, but it lies directly below a lahar that is obviously part of the Ellensburg Formation (Fig. 7). The pumicitic, lahar portion of the Ellensburg Formation is generally considered to be older than 9 my, based on K-Ar dates and fossils, whereas the Thorp Gravel is dated at about 4 my (Waitt 1979). Far too few dates exist for these units. The pumicitic part of the upper Ellensburg Formation may be much younger; future studies may show that, based on age, the Thorp gravel should not be considered as a separate unit but should be included as part of the Ellensburg Formation.

Ancestral Columbia River Gravels

Gravels deposited by the ancestral Columbia River can be found in the lower Yakima Valley. Recently, Swanson (pers. comm. 1979) suggested that Columbia River gravels also crop out beneath intercanyon basalt flows on the south side of the Yakima Ridge near Yakima. Fig. 9 compares three Columbia River gravel sites in the lower valley with gravels from Swanson's localities on Yakima Ridge, and with a single site from the middle Ringold Formation at Richland.

The ancestral Columbia River gravels in the lower valley (also known as the Snipes Mountain conglomerate and the Hood River gravels) contain abundant quartzite (40-60 percent) and small amounts of basalt. Andesite clasts are similar to those found in gravel of the Yakima River, and no distinctive volcanics or other indicators are present. The gravels lie near the base of the upper Ellensburg Formation above the Elephant Mountain basalt flow. Few rhyodacites are found in the Columbia River gravels, and the clasts are highly weathered and rounded. Basalt weathering rinds reach 20 mm in thickness, and andesites and granitics are highly weathered and often crumbly.

In comparison, the gravels found along Yakima Ridge beneath intercanyon flows contain less than 10 percent quartzite and compare more closely with modern Yakima River gravels and terraces. Gravel from the Middle Ringold Formation also does not match the ancestral Columbia River gravels occurring in the lower Yakima Valley. Webster (pers. comm. 1979) has suggested that the Middle Ringold gravels may have been deposited by an ancestral Snake River rather than by the Columbia River. These problems in correlation may be solved with additional sampling of the modern Columbia River, Middle Ringold Formation, and ancestral Columbia River gravels.

Conclusion

As a result of this study, the following conclusions can be drawn:

Sampling. In spite of the small number of clasts counted, composition percentages are quite similar for each size range. There are slightly more granitics present in the 8-25 cm fraction, and the accuracy of identification of individual clasts decreases slightly with the age of the gravel. This study shows that bulk sampling of gravel will give as good results as splitting into various size fractions.

Composition. The modern Yakima River downstream from Ellensburg, Washington, is influenced by four downstream sediment sources: Naches River sediment, ancestral Columbia River gravels, landslide deposits along the Horseheaven Hills, and Spokane Flood gravels. Naches River detritus is indistinguishable from that of the Yakima River. The percentage of pink and grey rhyodacites in gravel deposits can be used effectively to separate Yakima River terrace gravels, Thorp gravels, and gravels of the Ellensburg Formation. Weathering rind thickness on basalt clasts is helpful in determining relative ages of gravels but rinds on andesite are not useful.

Correlation. The Lakedale and Thorp terrace levels previously described in the upper Kittitas Valley can be identified downstream as far as Toppenish by using a combination of morphology, composition, and weathering characteristics. Terrace outcrops downstream from Toppenish are masked or destroyed by flood deposits and landsliding.

Columbia River. Attempts to correlate ancestral Columbia River gravels by composition yield confusing results. More sampling is needed to effectively correlate these gravel deposits.

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An Examination of Snap-trapping Techniques for Estimating Rodent Density in High Desert

Abstract

From September 1975 to May 1976, several variables that affect estimation of relative abundance of small mammals were examined on the Idaho National Engineering Laboratory Site in southeastern Idaho. Snap-trap transects were placed in uniform habitats to test the effects of: 1) trap type, 2) prebaiting traps, and 3) the length of the trapping period. The results indicated that Museum Special snap traps were more efficient than McGill rat traps with expanded treadles at capturing most small mammals. Larger rodents were taken in greater numbers by McGill traps with expanded treadles. Stations with two traps of one type were more efficient than stations with three, probably because of the lower probability of capture per trap at three-trap stations. The practice of prebaiting appeared to decrease variability in the catch, but the effect decreased when trapping was extended for periods greater than 3 days. Trapping periods of 3 to 5 days appeared to be sufficient for estimating the actual resident species composition and relative density of rodents.

Introduction

Accurate estimation of animal density is essential in analysis of ecosystem dynamics. Because most small mammals are secretive, estimates of population density are usually derived by indirect enumeration with snap traps. Numerous investigators have studied some of the variables that influence the probability of capture of small mammals (Gentry *et al.* 1966, Janion and Wierzbowska 1970; Smith and Blessing 1969; Weiner and Smith 1972; Gurnell 1976; Hansson 1967, 1974), but these studies have been largely restricted to non-desert species. Thus, although the probability of capture is known to be influenced by critical differences in species behavior, habitat, climate, prior trap occupancy, or trap type, a separate examination of the critical variables appears to be necessary in each geographical region. Further, although standardized techniques are available for use in estimation of relative density (Wheeler and Calhoun 1967, Grodzinski *et al.* 1966), variations in species composition among geographical areas affect the commensurability of estimates of abundance.

The purpose of this paper is to evaluate various trapping techniques to establish a reliable method for estimating abundance of small mammals in desert communities. Specifically, we report information on importance of trap type, on arrangement and com-

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binations of trap types used at trapped sites, on length of the trapping period, and on effect of prebaiting.

Study Area

The Idaho National Engineering Laboratory (INEL) Site is typical of the Great Basin or cool desert scrub biome. In all areas sampled during the course of this study, sagebrush-grass communities were dominant. Homogeneity of the habitat was qualitatively assessed by observing relative height and percent composition of vegetation at trapping sites. All of the transects were established in the areas that have not been grazed since 1950. A complete description of the Site can be found in Harniss and West (1973) and McBride *et al.* (1978).

Methods

Two types of break-back traps were used in this study. All traps were baited and rebaited whenever necessary with a peanut butter, rolled oats, and bacon grease mixture. Traps were set within 1 m of each station and were checked in the morning. All captures were recorded as to species, trap type, and station of capture.

Experiment 1 (Station Composition)

Experiment 1 was conducted on 13-15 September 1975. Trapping was conducted on 52 transects spaced every km on alternating sides of secondary roads on the INEL. Transects were placed perpendicular to the road and contained 10 trapping stations placed at 10 m intervals. Stations were set with one of five trap combinations: 1) two McGill rat traps with expanded treadles (Carley and Knowlton 1971); 2) three McGill rat traps; 3) two Museum Special break-back traps; 4) three Museum Special break-back traps; or 5) one Museum Special and one McGill. The sequence of the station combinations on the transects consisted of alternating between stations with two McGills and stations with one of the other combinations. Therefore, each combination was tested on at least 13 transects and on both sides of the road. Additionally, transects were alternated so each combination was repeated every fifth line. All traps were left in place and checked for 3 successive days. The objective of the experiment was to evaluate the effectiveness of various combinations of traps.

Experiment 2 (Prebaiting)

Experiment 2 was initiated in spring during 19-21 April 1976. The purpose was to test the effectiveness of prebaiting after we established what be believed was the best combination of traps that should be used. Eight line transects were placed in homogeneous habitat and consisted of 25 stations with 10 m separation and two Museum Special traps and one modified McGill per station. Lines were placed perpendicular to a section of secondary road 1 km apart on alternating sides. Four lines were prebaited daily for 3 consecutive days, and the remaining 4 lines were placed out for 3 days unbaited before they were baited and set to catch. Trapping was then conducted for 3 days.

Experiment 3 (Length of Trapping)

Following completion of Experiment 2, Experiment 3 was initiated to compare results of prebaiting with those obtained in Experiment 2 and to test the effectiveness of extend-

ing the length of trapping time. The trapping set up was identical to Experiment 2, except that 4 lines were run for 10 consecutive days. Two lines were prebaited for 3 days, then all traps were set and checked daily from 21 to 30 May 1976.

Results

A total of 8310 snap-trap night were expended in Experiments 1-3. The small mammals taken during these experiments, in order of decreasing abundance, were *Peromyscus maniculatus* (deer mouse), *Eutamias minimus* (least chipmunk), *Reithrodontomys megalotis* (western harvest mouse), *Onychomys leucogaster* (Northern grasshopper mouse), *Spermophilus townsendii* (Townsend's ground squirrel), *Dipodomys ordii* (Ord's kangaroo rat), *Perognathus parvus* (Great Basin pocket mouse), *Microtus montanus* (montane vole), and *Lagurus curtatus* (sagebrush vole). In the following text these species will be referred to by generic name.

Experiment 1

Table 1 presents the species of rodents obtained with various trap combinations during 3510 total trap nights. *Peromyscus* was the most abundant species (61.1 percent) captured. With regard to station composition, stations with two Museum Special traps (M.S.) proved to be the most efficient, catching 64 animals in 390 trap nights 16.4/100 trap nights). Stations with three M.S. were second in effectiveness followed by three McGill (M.G.) per station. The data were tested with a Chi-squared test of association for *Peromyscus* and *Eutamias*. No significant difference was detected in the catch ratios among trap combination s ($0.25 < P$ ($\chi^2 > 2.55$) < 0.50). The coefficient of contingency was $c = 0.14$. The same test applied to a comparison of the association between the two three-trap combinations, and the number of *Peromyscus* vs. *Eutamias* taken was highly significant ($0.01 < P$ ($\chi^2 > 5.12$) < 0.025). The coefficient of contingency was $c = 0.25$. The level of association in densities per 100 trap nights among independent populations of five of the six species taken (*Microtus* excluded) and the five trap combinations (see Table 1) was tested with a Kendall coefficient of concordance (Siegel 1956:229). The null hypothesis was that these five rodent species have no community of preference to the five trap combinations. This null was rejected ($W = 0.83$, $N = 5$, $K = 5$ and $P < 0.01$).

From the data, we concluded that for all species except *Dipodomys* and *Onychomys*, the two M.S. stations were the most effective. Stations with three M.G. were most effective for kangaroo rats and grasshopper mice, catching 0.85 and 1.03 per 100 trap nights, respectively, compared to 0.50/100 trap nights for *Onychomys* and zero for *Dipodomys* in two M.S. stations.

Experiment 2

The 1800 trap nights involved in Experiment 2 resulted in the capture of 97 animals, or 5.4 animals per 100 trap nights. The species composition was similar to the previous experiments, but the diversity was greater.

Table 2 gives the total numbers of animals and the animals per 100 trap nights by species in prebaited and non-prebaited lines. More individuals of *Peromyscus, Eutamias, Perognathus*, and total animals were captured on prebaited lines (3, 4, 7, and 8) than transects without prebaiting, although *Spermophilus* and *Onychomys* did not seem to

TABLE 1. Relative densities/100 trap nights of small mammals captured with various trap combinations during Experiment 1. A total of 3510 trap nights occurred during the experiment.

Trap nights	3510 all			390			585			1560			585			390		
combination[1]	combinations			2 MS			3 MS			2 MG			3 MG			1 MS - 1 MG		
Species	N[2]	TN[3]	%[4]	N[2]	TN[3]	%[4]	N[2]	TN[3]	%[4]	N[2]	TN[3]	%[4]	N[2]	TN[3]	%[4]	N[2]	TN[3]	%[4]
Peromyscus	149	4.2	61	41	10.5	64	45	7.7	79	29	1.9	48	17	2.9	44	17	4.4	71
Eutamias	60	1.7	25	16	4.1	25	9	1.5	16	19	1.2	32	11	1.9	28	5	1.3	21
Onychomys	13	0.4	5	2	0.5	3	1	>0	2	3	0.2	5	6	1.0	15	1	>0	4
Perognathus	5	0.1	2	2	0.5	3	2	0.3	4	1	>0	2						
Dipodomys	14	0.4	6							8	0.5	13	5	0.9	13	1	>0	4
Microtus	3	>0	1	3	0.8	5												
Totals	244	7.0		64	16.4		57	9.7		60	3.9		39	6.7		24	6.3	

[1]MS = Museum Special trap
MG = McGill Rat Trap
[2] = Total number captured
[3] = Total number/100 trap nights (rounded to nearest tenth)
[4] = Percent composition of total catch (rounded to nearest whole number)

TABLE 2. Total number, relative density/100 trap nights for each species of small mammal in prebaited and non-prebaited trap lines during Experiment 2. Total trap nights = 1800.

Line Number	Prebaited										Non-Prebaited									
	3		4		7		8		Total		1		2		5		6		Total	
	#	#/100 TN	#	#/100 TN	#	#/100 TN	#	#/100 TN	#	#/100 TN	#	#/100 TN	#	#/100 TN	#	#/100 TN	#	#/100 TN	#	#/100 TN
Peromyscus	12	5.3	12	5.3	12	5.3	13	5.8	49	5.4	5	2.2	9	4.0	7	3.1	6	2.7	27	3.0
Eutamias	2	0.9	1	0.4					3	0.3									0	0
Reithrodontomys					1	0.4			1	0.1					1	0.4			1	0.1
Spermophilus					1	0.4			1	0.1	1	0.4	1	0.4	1	0.4			3	0.3
Perognathus	1	0.4	2	0.9			1	0.4	4	0.4	1	0.4							1	0.1
Onychomys	1	0.4					1	0.4	2	0.2	1	0.4	1	0.4					3	0.3
Others									0	0.0							2	0.9	2	0.2
Totals	16	7.1	15	6.7	14	6.2	15	6.7	60	6.7	8	3.6	11	4.9	10	4.4	8	3.6	37	4.1

respond to prebaiting. A variance ratio test was performed to determine if the catch of rodents in the four non-prebaited lines was more variable than the catch in prebaited lines (Zar 1974:102). The catch was more variable in unprebaited lines [$0.10 < P(F_{3,3} > 3.36) > 0.25$].

Experiment 3

The species composition after 10 days (3000 trap nights) was: *Peromyscus*, 62.1 percent; *Eutamias*, 14.5 percent; *Onychomys*, 1.6 precent; *Perognathus*, 2.1 percent; *Reithrodontomys*, 11.3 percent; *Spermophilus*, 6.8 percent; others 1.6 percent. Table 3 gives the total number of animals removed and the number per 100 trap nights after 3, 5, 8, and 10 days. There is an obvious decline in the capture per unit effort. After the third day of trapping, the total catch never exceeded 34 animals or went under 23 (Table 4). Unlike total catch per day, species composition changed through time. *Peromyscus* was dominant throughout the trapping period, but after day 3 several changes took place. *Reithrodontomys*, the smallest rodent captured, increased from 6.6 percent after 3 days cumulative data to 25.0 percent on day 4 (Table 5). From day 4 to day 10 *Reithrodontomys* was above 11.0 percent on all days but day 5. Day 5 was the last day *Perognathus* was caught. Other species remained at about the same percent throughout the trapping.

Data in Table 6 compares prebaited lines with non-prebaited lines. The total catch per 100 trap nights was greater in the prebaited lines throughout the 10 days. The effect of prebaiting appeared to decrease from a nearly two to one advantage on day 1 to only a single animal advantage on days 6 through 10. Prebaited lines captured more animals on days 3, 6, and 9. The effect after 10 days was that prebaited lines captured 0.93 more animals per 100 trap nights. After 3 days, however, the prebait effect was much stronger. Prebaited lines caught an average of 3.77 more animals per 100 trap nights than the regularly treated lines. The greatest difference in species was for *Spermophilus*, where 23 animals were trapped on prebaited lines as opposed to three on regularly treated transects.

Discussion

Seasonal Considerations

The species composition observed during our study was similar to that described previously for the INEL Site (Allred 1973), but our data also provided an estimate of relative abundance. Our data support the findings of Larrison and Johnson (1973), who indicate that peak catches of *Peromyscus* occur during spring in Idaho. The cause of these peaks could result from either increased density (Briese and Smith 1974), trap response (Hansson 1967, Pucek 1969), or a seasonal change in species composition that affects trappability. Additionally, studies have shown that capture rates are higher during the breeding season (Chelkowska 1967, Gliwicz 1970).

Although our experiments were undertaken in what we concluded were uniform undisturbed stands of vegetation, it remains to be established to what degree changes in microhabitat may have affected the distribution of species available to our sampling systems. However, since our procedures were always completed on replicated transects, we believe that any minor local differences should not have affected the overall trends that we have been able to document.

TABLE 3. Relative densities of small mammals/100 trap nights after 3, 5, 8, and 10 days of trapping during Experiment 3. Total trap nights = 3000.

Total days trapped	3		5		8		10	
Species	Cumulative catch	#/100 TN	Cumulative catch	#/100 TN	Cumulative catch	#/100 TN	Cumulative catch	#/100 TN
Peromyscus	116	12.9	150	10.0	207	8.6	236	7.9
Eutamias	32	3.6	39	2.6	50	2.1	55	1.8
Reithrodontomys	12	1.3	20	1.3	33	1.4	43	1.4
Spermophilus	16	1.8	19	1.3	23	1.0	26	0.9
Onchyomys	1	0.1	3	0.2	3	0.1	6	0.2
Perognathus	6	0.7	8	0.5	8	0.3	8	0.3
Others	0	0.0	1	0.1	5	0.2	6	0.2
Totals	183	20.3	240	16.0	329	13.7	380	12.7

Trap Type

In the comparison of trap deployment, stations with two Museum Special snap traps were most efficient, followed by stations with three Museum Specials. These findings agree with previous studies (Wiener and Smith 1972) that Museum Special traps are more efficient than other types of snap traps and that two is the optimum number of traps per station for catching small mammals. The presence of larger species such as *Dipodomys* and *Spermophilus* and the higher catch of these in McGill rat traps necessitated, in our opinion, the partial use of the McGills.

Museum Specials appeared to be more efficient in catching smaller animals as a result of a more sensitive trigger mechanism than the larger rat traps. Apparently the reason two traps were more effective than three was a result of a lower probability of

TABLE 4. Total number (a) and relative density/100 trap nights (b) of all small mammals collected each day during Experiment 3. Data are presented for individual trap lines and are rounded to the nearest whole number. Lines 1 and 2 were prebaited 3 days, lines 3 and 4 were non-prebaited.

Day	Line 1	Line 2	Line 3	Line 4	Totals
1	19 (a)	42	16	16	93
	25 (b)	56	21	21	25
2	9	19	12	16	56
	12	25	16	21	15
3	4	7	13	10	34
	5	9	17	13	9
4	6	7	4	7	24
	8	9	5	9	6
5	6	11	5	11	33
	8	15	7	15	9
6	4	7	9	12	32
	5	9	12	16	9
7	3	10	4	6	23
	4	13	5	8	6
8	8	11	6	9	34
	11	15	8	12	9
9	4	8	11	4	27
	5	11	15	5	7
10	3	9	6	6	24
	4	12	8	8	6
Totals	66	131	86	97	380
	9	17	11	13	13

capture per trap at three trap stations, a condition previously noted by Andrzejewski *et al.* (1966). Thus, we selected two Museum Specials and one McGill rat trap as the station combination that would result in efficient catches representing all species during our spring experiments.

Baiting

The presence or absence as well as the type of bait explains part of the variability in trap response found in many studies (Smith *et al.* 1975). Certain kinds of bait elicit

TABLE 5. Number of small mammals captured and the percent composition (to nearest whole number) each day during Experiment 3.

Day	1		2		3		4		5		6		7		8		9		10	
Species	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Peromyscus	49	53	38	68	29	85	14	58	20	61	20	62	13	57	24	71	15	56	14	58
Eutamias	25	27	6	11	1	3	1	4	6	18	4	12	6	26	1	3	3	11	2	8
Reithrodontomys	7	8	3	5	2	6	6	25	2	6	5	16	4	17	4	12	5	19	5	21
Spermophilus	9	10	6	11	1	3	1	4	2	6	2	6			2	6	2	7	1	4
Onychomys	1	1					1	4	1	3							2	7	1	4
Perognathus	2	2	3	5	1	3			2	6										
Others							1	4			1	3			3	9			1	4
Totals	93		56		34		24		33		32		23		34		27		24	

a higher trap response than others, and these responses vary with species, age, sex, season, and habitat (Fowle and Edwards 1954, Fitch 1954, Patric 1970).

Because several species existed in the habitats that were sampled, there should be several different preferences in bait, and our choice of bait may have directly affected the probability of capture. For example, populations of *Onychomys* have been shown to be underestimated when rolled oats were used as bait (Larrison and Johnson 1973). Pinter and Negus (1965) have shown that green vegetation is important in the initiation of breeding in some rodents, and this phenomenon may cause a seasonal shift in bait preference.

The practice of prebaiting has been widely used (Grodzinski *et al.* 1966; Zejda and

TABLE 6. Total number (a) and relative density/100 trap nights (b) of all small mammals collected each day during Experiment 3 in prebaited and non-prebaited trap lines.

	Prebaited		Non-Prebaited	
Day	Daily Catch	Cumulative Catch	Daily Catch	Cumulative Catch
1	61 (a) 40.7 (b)	0	32 21.3	0
2	28 18.7	61 40.7	28 18.7	32 21.3
3	11 7.3	89 29.7	23 15.3	60 20.0
4	13 8.7	100 22.2	11 7.3	83 18.4
5	17 11.3	113 18.8	16 10.7	94 15.7
6	11 7.3	130 17.3	21 14.0	110 14.7
7	13 8.7	141 15.7	10 6.7	131 14.6
8	19 12.7	154 14.7	15 10.0	141 13.4
9	12 8.0	173 14.4	15 10.0	156 13.0
10	12 8.0	185 13.7	12 8.0	171 12.7
Total		197 13.1		183 12.2

Holisova 1970, 1971) to increase the probability of capture by conditioning the animal to trapping sites (Smith *et al.* 1975). In animal removal experiments, prebaiting decreases variation in the species taken, accelerates the rate of capture, and decreases variation in the rate of capture (Gentry *et al.* 1971). Seemingly, these reasons suffice to use prebaiting as a preliminary to animal-removal trapping. Data from our study suggested that when transects were trapped for more than 3 days, the effect of prebaiting decreased to a point where it was probably unnecessary. Therefore, we conclude that for short term removal studies in desert habitat similar to that found on the INEL

site, estimates of rodent density will be more accurate if the snap traps have been prebaited.

A disadvantage of prebaiting could result from abnormal animal concentrations at sampling sites, or disruption of the spatial organization of species within communities involved, thus inflating estimates of density (see Zejda and Holisova 1970). Since prebaiting is common in many population studies of small mammals, a study of the consequences of disruption of spatial organization on estimates of density needs to be completed for desert rodent communities.

Census Duration

An inherent assumption that the probability of capture declines with the length of censusing occurs in studies that employ removal censusing. Theoretically, in a given area, a certain percentage of the population will be removed during each census day until the area has been completely trapped out. Regression formulae (Hayne 1949) used in calculating relative densities are encumbered by this assumption. Experiment 3 indicated that if trapping exceeded 3 days, the capture per unit effort remained fairly consistent. This observation may have been a result of either a consistent number of individuals moving into the area vacated by the removal or inefficiency of traps in removing all the resident animals. We analyzed this problem and have presented the results elsewhere (Johnson and Keller 1983).

Recommendations

On the basis of the findings in this study, the following recommendations are offered for obtaining estimates of relative density of rodents in high desert communities:

1. Maximum rodent abundance in desert systems will probably be more adequately assessed if sampling is undertaken during spring.
2. Expanded treadle rat traps (Carley and Knowlton 1971) do not effectively sample rodent composition and density. Two Museum Special and one expanded treadle rat trap per station are recommended.
3. Baited, unset snap-traps should be placed at each sample station for several days prior to snap trapping. The bait used in all samplings should be consistent from year to year.

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Seedfall under Coastal Douglas-fir Shelterwood Stands

Abstract

Natural seedfall under Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) shelterwood stands provides both benefits and costs to the land manager, partly depending on resultant stand density. Under lean seedfall conditions, on the average, natural seedfall has the potential to restock 480 seedlings per acre within 3 years.

Introduction

Natural seedfall under coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) shelterwood stands provides both benefits and costs that should be considered by land managers planning for regeneration and early management of such stands. The major benefit is assurance of at least adequate[1] regeneration when site preparation is adequate (Williamson 1973). Also, natural seedlings should be better adapted than planted seedlings to adverse conditions (e.g., root pathogens and frost) peculiar to the site. Some benefits may be realized through genetic improvement if seed is provided by the most vigorous and dominant trees from the initial stand.

If planting of seedlings after the seed cut in shelterwood operations is planned, then the only direct cost associated with seedfall and resulting natural regeneration would be for precommercial thinning if seedling density is too great. Planting is commonly practiced under shelterwood stands to shorten the regeneration period. If survival of planted trees is good and natural seedlings are abundant, precommercial thinning may be necessary. With natural regeneration, on the other hand, insufficient density may result in a cost for fill-in planting.

Methods

Seedfall was measured under five shelterwood stands and one seed-tree stand, plus uncut stands adjacent to each cut stand (Fig. 1), beginning the first year after the seed cut. Collections started with two shelterwood units (Beeline and Deadhorse 6-2) and one seed-tree unit (Deadhorse 31-3) in southwestern Oregon, on the Tiller Ranger District of the Umpqua National Forest. The seed-tree unit was quite open initially and became more open through extensive windthrows of overstory trees. Measurements on these three areas began with the 1971 seed year. Beeline only included the seed years 1971 and 1972; the other two areas extended through the seed year 1975. A shelterwood study on the H. J. Andrews Experimental Forest (Hi-15), in the mid-Oregon Cascades, began providing data in 1975. An additional area on the Tiller Ranger District (Six

[1]As defined by the *Forest Service Handbook*, 2409.26d, appendix 64, Douglas-fir.

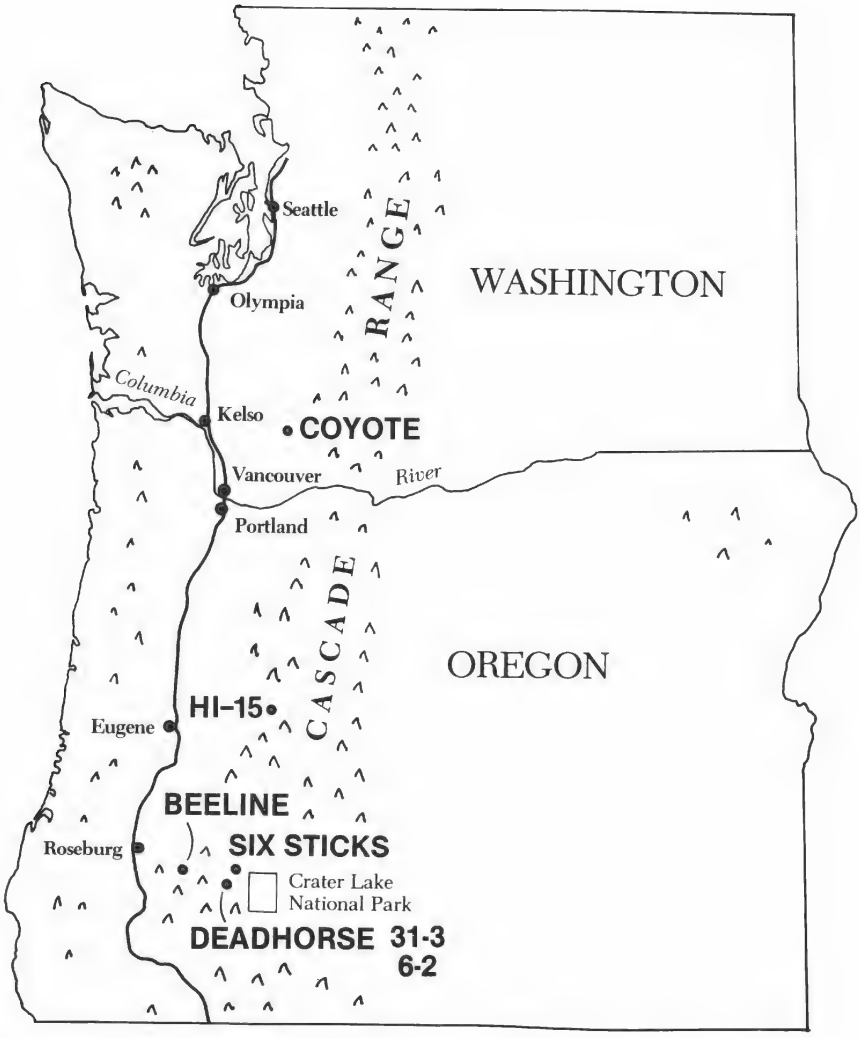

Figure 1. Six areas where shelterwood seedfall was studied.

Sticks) and one on the St. Helens District of the Gifford Pinchot National Forest (Coyote) provided data starting in 1976. Measurements were continued on these last three areas through seed year 1978. Overstory stand characteristics for each cutting unit were recorded (Table 1). All initial stands were on gentle topography, well stocked, and mature—with Douglas-fir predominant. None were considered overmature.

Seedfall was measured on or near the 15th of December, April, and August of each seed year by placing seed traps in the stands. Seed traps were 1 by 2 feet; no trap

TABLE 1. Characteristics of the shelterwood stands where seed was measured.

Unit	Location	Stand characteristics				Residual stand		
		Approximate age	Size	Traps per shelterwood unit	Year cut	Trees	Avg. diameter	Basal area
		Years	Acres	Number		No./acre	Inches	Feet/2acre
Beeline	T29S,R1W,S9	200	61	22	1969	15	32	85
Deadhorse 6-2	T31S,R2E,S6	200	24	13	1969	15	32	85
Deadhorse 31-3	T30,R2E,S31	300+	50	26	1969	4	41	37
Six Sticks	T29S,R2E,S23	300+	43	20	1976	8	60	157
Hi-15	T15S,R5E,S14	140	38	21	1974	45	24	140
Coyote	T8N,R6E,S36	300+	29	20	1975	18	37	134

1All based on Willamette Meridian.

TABLE 4. Total sound seed per acre (thousands) during regeneration period and live seedlings per acre for two shelterwood stands in southwestern Oregon.

Study area	Seed	Seedlings	Ratio
Beeline	216	245	882:1
Six Sticks	642	520	1235:1

was placed closer than 2 chains to a cutting boundary. The trap pattern for all areas was similar to that for the Beeline area.

In the laboratory, seeds were separated by species and counted. Potential viability was estimated in cut seeds; viability was assumed if seed coats were intact and seed interiors were full, firm, and white, with no indications of unfirmness, milkiness, or necrosis. The cutting test may be as good an estimator of viability of this seed as are the more sophisticated laboratory tests (Stein 1967, Bonner 1974).

Natural seedlings were available for the Beeline and Six Sticks areas only, from regeneration surveys by the Tiller Ranger District. These systematic surveys used a 4-milacre quadrat; 1 percent of the area was sampled in February 1980.

The data on Douglas-fir seedfall were analyzed as a paired-plot experiment with 4 degrees of freedom ($p = 0.1$). Deadhorse Unit 31-3 was not included in the analysis because it differed too much from the other units in overstory density. Data for other conifer species were not analyzed.

Results

Douglas-fir

Some seed was provided by both shelterwood and uncut stands almost every year (Table 2). The only year of complete failure was 1972. The difference in total seedfall between shelterwood stands and uncut stands was statistically nonsignificant ($t = 1.46$ with 4 degrees of freedom, $t_{0.1} = 2.132$) for the comparison of total seedfall in shelterwood stands to that in uncut stands.

Considerable variation in quantities of seed existed among different seed traps, areas, and seed years. This variation appears normal and in agreement with previous reports about Douglas-fir seedfall (Isaac 1943, Roy 1960, Reukema 1961). The seedfall in the seed-tree unit (Deadhorse 31-3) was only about half of that in the associated unit 6-2. The very wide spacing of the residual overstory had a major impact on seed production.

TABLE 2. Sound seed per acre (thousands) and sampling errors (p = .10), by study area, seed year, and treatment.

Area and species	1971 Uncut	1971 Shelterwood	1972 Uncut	1972 Shelterwood	1973 Uncut	1973 Shelterwood	1974 Uncut	1974 Shelterwood	1975 Uncut	1975 Shelterwood
Douglas-fir										
Beeline 22	193±75	214±45	0	2[1]						
Deadhorse 31-3 26	244±72	102±37	3[1]	1[1]	84±15	45±15	0[1]	12[1]	118±66	66±20
Deadhorse 6-2 13	304±102	211±88	3[1]	0[1]	96±73	76±25	7[1]	4[1]	68±28	117±37
Other conifers										
Beeline	317±208	35±11	0[1]	0[1]						
Deadhorse 31-3	—	—	0[1]	0[1]	0[1]	2[1]	0[1]	0[1]	72±124	3[1]
Deadhorse 6-2	—	—	0[1]	0[1]	5[1]	2[1]	13±15	8[1]	0[1]	0[1]

Area and species	1975 Uncut	1975 Shelterwood	1976 Uncut	1976 Shelterwood	1977 Uncut	1977 Shelterwood	1978 Uncut	1978 Shelterwood
Douglas-fir								
Six Sticks 20			154±84	113±29	17±12	22±10	388±84	507±87
Hi-15 21	39±12	29±25	5[1]	14[1]	0[1]	6[1]	35±17	124±27
Coyote 20			205±79	207±48	12±9	24±18	166±68	386±82
Other conifers								
Six Sticks			87±101	12±9	19±16	19±11	158±49	44±27
Hi-15	12[1]	3[1]	3[1]	0[1]	5[1]	1[1]	41±25	99±64
Coyote			174±108	9[1]	165±63	597±589	339±80	194±104

[1]Seedfall deemed too low to provide a reliable estimate of sampling error.

Seed production in the Hi-15 area was low relative to other areas, even in the generally better seed year of 1978 (124,000 sound seed per acre). In that year, the Coyote unit provided three times as much seed (386,000), and the Six Sticks unit, four times as much (507,000). All three stands contained vigorous, mature seed trees; no reason for the low seed production at Hi-15 is evident. Low production in three consecutive years at any particular area is probably not uncommon.

In the first year after the seed cuts, all five shelterwood stands produced from two-thirds to as much sound seed as did uncut stands (Table 3), although residual overstories had no more than half the number of dominants as did these uncut stands. By the second year and beyond, shelterwood seedfall generally was near or above that of uncut stands so that the five year totals were similar. These results suggest immediate and greater production of sound seed per tree in shelterwood stands than in uncut stands.

Natural seedling and sound-seed data for the Beeline and Six Sticks areas indicate seedling-to-seed ratios for these two units on gentle topography in the South Umpqua drainage of the Tiller Ranger District of about 1:1000.

Other Conifers

Most of the overstory trees in these shelterwood stands were Douglas-fir. Nevertheless, sound-seed production by other conifers—principally western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western redcedar (*Thuja plicata* Donn ex D. Don), with minor amounts of true firs (*Abies* spp.) and western white pine (*Pinus monticola* Dougl. ex D. Don)—was appreciable, though usually half or less of that provided by Douglas-fir. Undoubtedly, much seed of other species came from surrounding uncut stands, because these seeds are light and can be disseminated widely by winds.

The Coyote unit had many pole-sized western hemlock and western redcedar trees that evidently were unmerchantable and were not cut. These trees were responsible for this unit's having had more abundant seedfall from these species than the other units.

As with Douglas-fir, seed production by other conifers varied from area to area and year to year. For instance, for the Deadhorse units, even uncut stands had complete failures two years of four, with low seedfall in the other two years. In contrast, the uncut areas in the Six Sticks unit produced abundant seed all three years, and seedfall on the Coyote unit was abundant in two years and moderate in a third.

Discussion

The sampling errors (Table 2) range from about 17 to over 100 percent of the mean for Douglas-fir. Many more traps would have been needed to bring these errors down to, say, 10 percent of the mean. I had planned for a 10 percent sampling error (at least for good seed years), but variation was much greater than expected. Fortunately, the improvement in seed production by trees in shelterwood stands relative to that in uncut stands was consistent between areas and supports the statistical suggestion of no difference between treatments.

The Washington State Department of Natural Resources, the Oregon State Board of Forestry, and the U.S. Forest Service's Pacific Northwest Region cooperate annually in publishing cone-crop reports to provide seed gatherers and nurserymen with estimates of forthcoming seed supplies. No report during the period of this study predicted

TABLE 3. Sound seed per acre (thousands), by study area, seed year, and treatment.

Area and species	Year 1		Year 2		Year 3		Year 4		Year 5		Total	
	Uncut	Shelter-wood	Uncut	Shelter-wood	Uncut	Shelter-wood	Uncut	Shelter-wood	Uncut	Shelter-wood	Uncut	Shelter-wood
Douglas-fir												
Beeline	193	214	0	2							193	126
Deadhorse 31-3	244	102	3	**1**	84	46	0	12	118	60	(449)[1]	(221)[1]
Deadhorse 6-2	304	211	3	**0**	96	76	7	**4**	68	**117**	478	408
Six Sticks	154	113	17	**22**	388	507					559	642
Hi-15	39	**29**	5	**14**	0	6	35	124			79	173
Coyote	205	207	12	**24**	166	386					383	**617**
Other conifers												
Beeline	317	35	0	**0**								
Deadhorse 31-3	—	—	0	**0**	0	**2**	0	**0**	72	3		
Deadhorse 6-2	—	—	0	**0**	5	2	13	**8**	0	**0**		
Six Sticks	87	**12**	19	**19**	158	44						
Hi-15	12	3	3	0	5	1	41	99				
Coyote	174	9	165	597	339	**194**						

[1]Not included in analysis.

seed abundance above 4.2, on a scale of 1 to 5.[2] Seven years of the eight had predictions of a light crop or poorer. In spite of this dismal forecast, substantial amounts of seed (at least 20,000, or about half a pound per acre) were provided about every other year by these shelterwood stands. The overall average production of sound seed for the Beeline and Six Sticks shelterwood stands was 161,000, or about four pounds of seed, per acre per year. If one assumes a seedling/seed percentage of 0.1 (suggested by the regeneration surveys and seedfall data from these two shelterwood units), then three years' seed production might restock an area to about 480 seedlings per acre on gentle northerly slopes in the vicinity of the South Umpqua drainage under the standard site preparation techniques in use today, and under seed production circumstances that are probably typical.

With medium or heavy seed crops, and good site preparation, seeds can germinate and seedlings survive by the thousands under shelterwood (Williamson 1973). Thus, shelterwood regeneration may lead to overstocking. On the other hand, understocking may result from inadequate site preparation, insufficient control of competing vegetation, and careless logging practices during overstory removal. Research on these practices could lead to minimum costs for establishing regeneration whenever shelterwood harvesting is practiced.

The results presented here agree with previous reports concerning thinning effects on Douglas-fir seedfall (Reukema 1961) and seed production by seed-tree stands (Garman 1955), which indicated not only the variation in seed production between areas and years, but also increased production per tree in partial-cut stands compared to uncut stands, except in years of seed failure.

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[2]The cone-crop scale is: 1—failure, 2—very light, 3—light, 4—medium, and 5—heavy.

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Further Notes on the Shore Flies (Diptera: Ephydridae) of Mount Rainier National Park, Washington[1]

Abstract

Information is presented concerning the species composition and habitat distribution of the shore flies (Diptera:Ephydridae) of Mt. Rainier National Park, Washington. A total of 59 species in 22 genera was collected during the period 1977-1979. Seasonality, relative abundance, and biological findings are given for 33 species. Abundance and habitat data are presented in tabular form for all species encountered. *Notiphila pallidipalpis* Cresson and *N. sicca* Cresson are recorded as new Washington state records.

Introduction

Shore flies are among the most prominent members of aquatic and semiaquatic environments. They are especially abundant along the margins of many alkaline and saline ponds that are common throughout portions of the northwest. In many instances, they are the only insects which have the ability to colonize and survive in these unusual habitats. However, they are not restricted to saline and alkaline waters, and most species are found in freshwater situations.

Taxonomically, the family is comprised of over 1200 world species, approximately 400 of which are known to occur in America north of Mexico (Deonier 1979). Of this number, slightly more than 150 species have been collected in the Pacific Northwest.

In 1979, I presented a preliminary report on my findings concerning the habitat distribution of the shore flies within Mt. Rainier National Park (MRNP) of west-central Washington (Zack 1979). Since then, a number of previously unreported species have been collected, and I have found it necessary to modify and add to the habitat types occurring in the Park.

Methods and Materials

During the years 1977-1979, eighteen trips were made to Mt. Rainier National Park (MRNP), for a total of 56 collecting days. MRNP is characterized by unpredictable and extremely variable weather, and thus a consistent collecting regimen was not established. The area proved most accessible and productive from mid-June through September. Periods of two to five days were spent within MRNP on each trip, and during any given trip, attempts were made to collect from each habitat type at least once. Doing so was often difficult, especially in the case of the more inaccessible habitats such as the montane seep, which was sampled once each month. The com-

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posite *Anaphalis margaritacea* (L.) B & H was sampled only during periods of bloom.

Adult flies were collected by sweeping predefined habitat types with a standard 12-inch aerial net. Flies were killed, layered into tins, and stored on dry ice until processing, which took place either in the Park or upon return to the laboratory in Pullman. Larvae were collected by sifting through vegetational debris, algal mats, mud, or other substrates in which they occur. They were placed in Kahle's solution for a period of two to three days and then transferred to 70 percent alcohol. Plant materials were placed into plastic bags and stored on dry ice until they could be returned to the laboratory for identification. Voucher specimens of adult ephydrids have been placed in the James Entomological Collection at Washington State University, the University of Minnesota Insect Collection, the United States National Collection, and in my own collection.

As in other studies of this type, preliminary sampling preceded the pin-pointing of habitats and was followed by intensive sampling throughout the field season. Initially, I had planned to use the habitat guidelines established in previous investigations (Deonier 1965, Scheiring and Foote 1973), but because of the diverse and unusual topography of the area these guidelines were not feasible. I have therefore defined the most important ephydrid habitat types occurring on Mt. Rainier.

Description of Habitat Types

Previously, I distinguished eight habitat types that were rather well delineated in MRNP (Zack 1979). Since then, I have added two and slightly modified one. These latter are discussed in some detail, whereas those that were previously described are only mentioned.

Moist Meadow Habitat Type

Previously I listed this habitat as the Hudsonian Moist Meadow. Although these meadows are more often associated with the Hudsonian Zone (approx. 1500-2100 m), they are not solely confined there, and similar locations in the Transition and Canadian Zones provided an equivalent composition of shore fly species.

Montane Seep Habitat Type

A series of wet, rockslide areas approximately 50 m long by 7 m wide with slopes of 40-45 percent comprise this habitat.

Sedge Meadow Habitat Type

The sedge meadow habitat consists of ponds and lakes with vegetation (mostly *Carex* spp.) either along the margins or covering the entire area.

Mud Shore Habitat Type

This habitat type was not previously used, as localities with mud shores were placed under the wet woodland or other designations. Upon more thorough examination, though, certain areas were found to contain a well-defined species composition. And although these areas proved to be variable, they are all best defined as mud shore habitats.

Although most of the glacially-fed pools and streams on Mt. Rainier have fine sand shores (glacial flour), two woodland pools, formed as a result of stream obstruction by beaver dams, were found to have extensive mud shores. These areas were high in organic matter and often contained abundant populations of unicellular algae and diatoms. However, no algal mat formation was found at any time during the study. Unlike other mud shore habitats, those at Mt. Rainier lasted throughout the season and were invaded only marginally by plants as the summer progressed. This lack of vegetational growth is probably a result of the short growing season at MRNP and the continual movement of snow-melt water through the area. The habitat supported a large, well-defined group of ephydrid species.

Stream Rocks Habitat Type

Another previously unreported habitat type, stream rocks localities, was examined only during the final year (1979) of the study. Two areas were sampled. The first consisted of a small stretch of shoal approximately 50 m long on the north side of the Paradise River, 1 km below Narada Falls. The second was a similar stretch of van Trump Creek slightly less than 3 km above Christine Falls. Vegetation, which was limited to unicellular and filamentous algae, diatoms and mosses, extended from below the surface of the water up into an area of the rocks that was continually being splashed and washed by stream flow. Luxuriant growths of diatoms formed in early spring and late fall. Flies were most commonly found at or slightly above the surface of the water.

Water speed seemed to play little part in the ability of the flies to colonize the habitat. Flies were found as long as the water was neither stagnant nor flowing so fast that the rocks were continually submerged. This habitat proved very susceptible to spring thaw, especially at the higher elevations, and may be unstable from year to year.

Glacial River Bed: Glacial Drift Type I Habitat Type

The habitat consisted of the beds of the major glacial rivers that flowed through the Park. Most extensively collected was the White River bed.

Sand Shore: Glacial Drift Type II Habitat Type

Sand shores along both ponds and streams were sampled. Water speed in these habitats was slow in comparison to the glacial river bed localities.

Roadside Ditch Habitat Type

Roadside ditch localities included both open and vegetation innundated excavations along both major and minor roadways. Areas at different elevations were sampled.

Flowering **Anaphalis margaritacea**

The flowers of *Anaphalis margaritacea* attracted four ephydrid species. Flowers were sampled during periods of bloom, July through August.

Habitat Distribution

In 1979, I reported 35 species in 17 genera as having been collected throughout MRNP (Zack 1979). Since then, two species have been deleted, while 26 have been added.

At present, a total of 59 species representing 22 genera has been found.

As in previous papers (Scheiring and Foote 1973; Zack 1979, 1982), the relative abundance of each species is calculated based on its percentage of the total number of specimens taken within the habitat. In all situations where only a single specimen was taken, the species is listed as rare (Table 1). Abundance figures were delegated as follows:

rare (r)	0-3 percent of the total catch/habitat
occasional (occ)	3-9 percent
common (c)	9-15 percent
abundant (a)	15-26 percent
very abundant (va)	26 percent and greater

In the next section, the species encountered in MRNP that were not discussed previously (Zack 1979) are listed. Table 1 is a listing of all species encountered throughout the three year period of study.

Results

Subfamily Psilopinae

Athyroglossa ordinata Becker. *A. ordinata* was collected only in the sand shore: glacial drift type II habitat, and in fairly low numbers. The species is Holarctic in distribution. Studies by Scheiring and Foote (1973), who worked in northeastern Ohio, found it to be a rare inhabitant of the grass shore habitat, while Deonier (1965) in Iowa, captured specimens in the sand shore and stream rocks habitats. On Mt. Rainier, I collected specimens only in mid-July.

Allotrichoma sp. Few specimens of *Allotrichoma* were taken from late June to early August. The genus is in need of revision, and specific determination is difficult. Most were collected by sweeping the shoreline of a small Canadian Zone moist meadow stream.

Ditrichophora subnubila Cresson/*D. tacoma* Cresson. Originally (Zack 1979), I listed these species separately, and although both are recorded as occurring in the vicinity of MRNP, with more specimens, I found it impossible to separate the two based on the characters used by Cresson (1942). Specimens were taken in a variety of habitats from late June through mid-August.

Psilopa compta (Meigen). Holarctic in distribution, *P. compta* was the most abundant of the shore flies in the sedge meadow habitat. The species appeared in early August when the depth of the water in the meadow had stabilized and water flow through the meadow became negligible. (Most of the sedge meadows are fed by small to medium-sized streams of snow-melt origin that may cause extreme turbulence in the habitat during spring and early summer.) Adults were most easily collected by aspirating them from the stalks of living or clumps of decaying vegetation that often became caught in the sedge.

Mating was observed on two occasions, both taking place on decaying vegetation lying upon the surface of the water. Courtship behavior appeared extremely limited, with the male approaching the female from behind and leaping onto her back. This behavior is not unusual, as the same type of courtship has been found in *Parydra* (Clausen and Cook 1971), *Discocerina obscurella* (Fallén) (Foote and Eastin 1974),

and other ephydrids. In the case of *Psilopa compta*, if the female was receptive, she would spread her wings, thus allowing the male to initiate copulation. If not receptive, she would fold her wings over her back, making it impossible for the male to maintain contact and eventually causing him to dismount.

In mid-August, two-third instars of *P. compta* were found by sifting through the vegetational debris caught between the sedge. Both pupated at the laboratory in Pullman. Adult eclosion took place in five and six days.

In Iowa, Deonier (1965) found *P. compta* to be a rare inhabitant of the sedge

TABLE 1. Habitat distribution of Mt. Rainier shore flies.[a]

Species	Moist meadow	Wet woodland	Montane seep	Sedge Meadow	Mud shore	Stream rocks	Glacial river bed	Sand shore	Roadside ditch	Anaphalis margaritacea
Athyroglossa cressoni								r		
A. ordinata								r		
Allotrichoma sp.	occ				r			r		
Discocerina obscurella	r				r			occ		
Hecamedoides glaucella								r		
Ditrichophora argyrostoma	a	va			r	r		c	r	a
D. occidentalis					r			occ		
D. subnubila/D. tacoma	occ	occ			r	occ		r	r	
Polytrichophora orbitalis								r		
Psilopa compta	r			va				r		
P. olga				r						
Hydrellia griseola	va	r		r	occ			c	occ	va
Hydrellia lata					va			r		
H. platygastra	r			c	c			r		
H. proclinata	occ				r			r	a	
Philygria debilis	r	r			r			r		a
P. nigrescens								r		occ
Ilythea caniceps				r						
I. spilota	r							r	r	
Ilythea sp.									r	
Notiphila aenigma				r				r		
N. avia				r	r					
N. pallidipalpis					r					
N. sicca				r						
N. uliginosa	r			r						
N. caudata sp. gr.					r					
Parydra acuta		occ	r			r				
P. alpina					occ		r			
P. appendiculata					r			r		
P. aquila								r	r	
P. borealis								r	r	
P. copis					r					
P. halteralis	r	c	c		r				c	
P. incommoda	r								r	
P. pedalis		r			occ			r	r	
P. quadriloba	r	occ		r					occ	
P. socia		c	r		c	va		r	occ	
Hyadina binotata	r				r			r		
H. cesta				r	r					
Lytogaster gravida		r			r			r	r	
Pelina truncalata latiforma				r						
Oethera acta				r				r		

TABLE 1. (Continued)

O. collina						r			
O. occidentalis			r						
Paracoenia platypelta	r							r	
Lamproscatella occidentalis	r	r	r					r	
Scatella laxa	occ		occ	occ			r	occ	
S. paludum	r	occ		r			a	r	
S. pentastigma	occ	r	c	r			occ	c	
S. picea									r
S. stagnalis	occ	r	a	a		r	a	c	
S. troi					occ				
Limnellia halioptera		c							
L. rainier	r								
L. turneri	r			r				r	
Scatophila despecta					occ				
Scatophila sp. A.	r							r	
Scatophila sp. B.						occ			
Scatophila sp. C.	r								

[a]Letters indicate relative abundance; va=very abundant, a=abundant, c=common, occ=occasional, r=rare.

meadow and *Eragrostis* mat habitats. The species was not collected by Scheiring and Foote (1973) in Ohio. Throughout eastern Washington the species is extremely common, especially in both the sedge meadow and cattail marsh habitats.

Psilopa olga Cresson. Only a single specimen of *P. olga* was obtained during the study and was collected in the same habitat as *P. compta*, again in mid-August. The species was collected in the sedge meadow and limnic wrack habitats of Iowa (Deonier 1965).

Subfamily Notiphilinae

Hydrellia lata Cresson. A large series of what appears to be *H. lata* was collected rather commonly, especially in the mud shore habitat, throughout late June to early August. Most specimens were obtained by sweeping the vegetation free margin of a small beaver pond that had formed under a heavy forest canopy. Specimens were taken all the way from the waterline to approximately 1 m out from it. Although a short search was conducted for the larvae and thus a host plant, neither were located.

Specimens were identified using the key provided by Deonier (1971) in his revision of *Hydrellia.* As he had only females available to him, and as specimens were not available to me for comparison, my identifications must at this time remain tentative. Originally, the specimens discussed herein were thought to be *Hydrellia serena* Cresson (Zack 1979).

Hydrellia melanderi Deonier. A specimen originally thought to be *H. melanderi* (Zack 1979) proved to be *H. proclinata* Cresson. *H. melandri* should therefore be deleted from the MRNP species list.

Ilythea caniceps Cresson. *I. caniceps* seems to be a rare West Coast and Neotropical species (Wirth 1965). On Mt. Rainier, only a single specimen was taken from the sedge meadow habitat in early August. In a separate study of the eastern Washington ephydrids, I have collected *I. caniceps* from the cattail marsh and grass shore habitats, but only in sparse numbers. In these habitats, specimens were taken as early as February and as late as September.

Ilythea spilota (Curtis). Only three specimens of *I. spilota* were collected in the Park, each from a different habitat. These findings tend to agree with those of Deonier (1965) and Scheiring and Foote (1973), who found the species in no less than five different habitat types. Foote (1979) considered the species to be monophagous and largely restricted to diatoms. The concept of generalists and specialists among algal feeding shore flies and the effect of this on their abundance and distribution has been discussed by Foote (1977, 1979) and Zack and Foote (1978).

Ilythea sp. Only a single specimen of this unknown (probably new) species was taken in mid-August. The specimen cannot be identified using the presently available literature.

Notiphila aenigma Cresson. Two specimens were collected, one along a sand shore in late June and the second in the sedge meadow habitat during mid-July. The species occurs throughout the western United States and southwestern Canada (Mathis 1979). Both Mathis (1979) and Busacca and Foote (1978) discussed the biology of this species. The latter paper also contains descriptions of the immature stages.

Notiphila avia Loew. Specimens of *N. avia* were obtained in both the sedge meadow and mud shore habitats through the period June to early August. The species is encountered throughout northern North America, especially at higher elevations (Mathis 1979).

Notiphila pallidipalpis Cresson. The finding of *N. pallidipalpis* represents a new state record for Washington. At Mt. Rainier only a single specimen was collected in the mud shore habitat. The species is widely distributed throughout the northern United States and southern Canada, especially from the Upper Great Lakes States eastward (Mathis 1979).

Notiphila sicca Cresson. Representing a new state record, only a single specimen of *N. sicca* was collected from the sedge meadow habitat in mid-August. Mathis (1979) considers it to be one of the more common of the western species, especially in the more arid regions. Although the species has been collected as far east as Ohio, it is most abundant throughout Utah, New Mexico, Arizona, and Colorado (Mathis 1979).

Notiphila uliginosa Haliday. Specimens of *N. uliginosa* were found in the sedge meadow and moist meadow habitat types. This species is widespread, occurring throughout the western United States and as far north as Alaska and east to Vermont (Mathis 1979).

Notiphila caudata species group. Mathis (1979) synonymized the genus *Dichaeta* with *Notiphila*, reducing those species previously placed in the genus *Dichaeta* to a species group in *Notiphila*. A revision of the group is being planned (Mathis, pers. comm.). Only two specimens were collected, both in the mud shore habitat.

Parydra alpina (Cresson). The type locality of *P. alpina* is Longmire Springs, Mt. Rainier. The species is predominately northern, occurring from Washington to New Hampshire. On Mt. Rainier, *P. alpina* was encountered almost exclusively in the mud shore habitat during June through August. The habitat consisted of a small, well-shaded stream with a 2 to 3 m mud shore on either side. The shoreline of the stream was slightly spotted with vegetation, but still had extensive areas that were vegetation free. Continually in shade, the stream ran through a heavily wooded area. This situation is in contrast to the more open mud shore habitat, only 10 m away, in which the closely related species *P. pedalis* Clausen was found. This latter mud shore had extensive periods of exposure to sunlight, unlike the shaded mud shore on which *P. alpina* occurred.

Parydra appendiculata Loew. This is a common species occurring throughout most of the Nearctic Region (Clausen and Cook 1971). Deonier (1965), in Iowa, found the species to be common in seven of the 11 habitat types sampled by him. On Mt. Rainier, specimens were relatively scarce but were collected June through August in both the sand shore and mud shore habitats. In a separate study in the northwest (Zack, unpub.), the species was collected as early as February and as late as October in a variety of shoreline habitats, including the grass shore.

Parydra borealis (Cresson). Only two specimens of *P. borealis* were collected in MRNP during this study. Both were taken late in the season (August and September).

Parydra copis Clausen. This is a relatively rare species, thus far known only from coastal Washington and Oregon. Only two specimens were taken in the Park, both in August in the mud shore habitat type.

Parydra pedalis Clausen. *P. pedalis* is a relatively scarce species known only from British Columbia, California, and Washington (Clausen and Cook 1971, Clausen 1977a). For the most part, *P. pedalis* was confined to the mud shore habitat, although a few specimens were collected in other habitat types. The species was most common in late June, with specimens collected infrequently through mid-August. The largest collection was taken on the mud shore of a small pool that had formed as a result of beavers damming a small creek. The specimens were taken between the water and encroaching shore vegetation, a distance of approximately 1 m. Although the area was heavily wooded, it still received periods of extensive sunlight throughout the day, in contrast to the mud shore habitat in which *P. alpina* was found.

Hyadina binotata (Cresson). A widespread and relatively common species throughout most of North America, *H. binotata* was only occasionally collected in the Park. Specimens were taken from late June through early August. Both Deonier (1965) and Scheiring and Foote (1973) found the species in their studies. Deonier, especially, found it to be common. Foote (1977, 1979) has speculated that *H. binotata*, and in fact many species in the tribe Hyadini, may be limited to feeding on blue-green algae. An intensive study of the algal constituents of the habitat may help verify the hypothesis of Foote. It may be that a general lack of habitats in which blue-green algae are dominant serve to keep populations of *H. binotata* to a minimum in the Park.

Axysta cesta (Haliday). *A. cesta,* holarctic in distribution, reaches its southern limits in North America slightly south of the 45th parallel. On Mt. Rainier, specimens were collected June through August, most commonly in the mud shore habitat. Dahl (1959), in his study of the Scandinavian ephydrids, found the species to be a rare inhabitant of the maritime grass pool and reed vegetation habitat types.

Ochthera acta Clausen. This species is thus far known from the southwestern tip of British Columbia and the extreme northwestern United States (Clausen 1977b). As with all species of *Ochthera* collected, *O. acta* was rare in the Park, with only three specimens found. Individuals were taken in early June and August.

Ochthera collina Clausen. Only a single specimen of *O. collina* was taken in mid-July from the glacial river bed habitat. Throughout eastern Washington and northern Idaho, it is a relatively common species, especially in the cattail marsh and sand shore habitats.

Ochthera occidentalis Clausen. This species is probably the most common of the northwestern *Ochthera.* Within MRNP, only two specimens were taken in late August (from the sedge meadow habitat).

Subfamily Ephydrinae

Scatella picea Walker. A single specimen of what appears to be *S. picea* was collected in mid-July. This species was found by Melander in MRNP in the early 1900s, but I have not had a chance to examine these specimens. Perhaps the specimens that have been identified as *S. picea* are variants of *S. stagnalis* (Fallén) or *S. pentastigma* (Thomson).

Scatella troi Cresson. A relatively widespread species in the Pacific Northwest, *S. troi* seems to have well-defined spatial requirements. On Mt. Rainier, specimens were taken from July through September, but only in the stream rocks habitat. Adults were found exclusively in the small splash zone between the water surface and the dry upper surfaces of the rocks. Flies were constantly moving up and down the rocks following the fluctuations of the waterline. Adults continually probed the wet surface with their mouthparts, probably feeding on the abundant diatoms and unicellular algae occurring in the habitat type.

Mating, observed in a few rare instances, took place in the same habitat; it is comparable to that observed for *S. stagnalis* (Dahl 1959, Deonier 1972). The male uses a series of "wing scissorings" that initiate courtship. If the female is receptive, she responds with a similar series of wing scissorings, leading to eventual mounting by the male and copulation. Oviposition and larval development probably occur in the moss and filamentous algae that grow just at the surface of the water.

Several clinocerine empidids (Diptera: Empididae: Clinocerinae) and dolichopodids (Diptera: Dolichopodidae) were also found to be common in the area frequented by *S. troi.*

Limnellia rainier Mathis and Zack. A single specimen, the type, was collected in mid-July along a small snowmelt stream on the eastern boundary of the Park. The area was still under considerable snow cover. The species description and a more detailed habitat description are presented in Mathis and Zack (1980).

Scatophila despecta (Haliday). Three specimens of *S. despecta* were found in the stream rocks habitat in early August. The species is holarctic in distribution (Wirth 1965). Both Deonier (1965) and Scheiring and Foote (1973) list *S. despecta* as rare in Iowa and northeastern Ohio, respectively.

Scatophila species A. Seven specimens of an unknown species were collected in mid-July from the roadside ditch and moist meadow habitat types.

Scatophila species B. Zack (1979) recorded this shore fly as a new species of *Scatophila.* Specimens were collected from June through September, but never abundantly. This species was one of the very few found in the stressful glacial river bed habitat type.

Scatophila species C. A single specimen of a small unknown species was collected in the moist meadow habitat in late June.

Discussion

Distributional studies of shore flies have been conducted in other parts of the country. Deonier (1965), in his survey of the shore flies of Iowa, found 100 species in various habitats. Scheiring and Foote (1973), who surveyed northeastern Ohio, found a total of 68 species. In both of the preceding studies, the areas examined were extensive. In contrast, the large number of shore fly species (59) collected in the limited area of Mt. Rainier National Park is probably a result of the heterogeneity of the area. Although encompassing only 600 sq. km, approximately one-quarter of which is arctic-alpine terrain, the Park encompasses no less than four different life zones and contains most of the major habitat types (see Deonier 1979) in which ephydrids have been found. The existence of many areas in which a similarly large number of habitats are found in such a limited geographical area is doubtful.

The period during which areas of the Park are open to colonization and populational build-up are often limited. Temperature and precipitation differences at most places in MRNP are strongly related to elevation. Elevational effects expressed through temperature and precipitation are also major factors in delineating the critical period of habitat availability. The restricted season is especially evident in the Hudsonian Zone (1500-2100 m), which was under considerable snow cover until early or mid-July. In contrast, the major areas of the sand shore (glacial drift type II and sedge meadow habitats), which were at much lower elevations, were snow-free by mid-May and remained so until October or November. The low numbers of both species and individuals collected in some of the Hudsonian Zone sites may reflect the relatively short season. Although many seemingly ideal Hudsonian sites provided few specimens, similar sites at lower elevations often contained an abundance of both species and individuals. In the Transition (up to 900 m) and Canadian Zones (900-1500 m), the reduction in availability of habitat is not as pronounced as in the Hudsonian Zone, but depending on the specific site examined, must still be considered an important limiting factor.

I suspect that most of the ephydrid species encountered in MRNP have more than one generation per season. This supposition is based on the relatively short life cycle of from 2 to 3 weeks for most shore flies and the collection of individuals of many species throughout the field season. However, for species collected only at high eleva-

tions or only for short periods, especially late or early in the season, there may be a single generation. *Psilopa compta*, which was collected only in mid-August, *P. olga*, and possibly several species of *Parydra* are the most noticeable examples. Unfortunately, because of the low numbers of specimens examined, I lack sufficient data to verify the voltinism of many of these "rarer" species.

In general, the ephydrid species composition of Mt. Rainier is similar to that encountered throughout the more boreal areas of the Pacific Northwest. What is unusual is the number of varying habitats with associated ephydrid faunas occurring in such a limited geographic area. In addition, there are at least two species (*Parydra acuta* Clausen and *Limnellia rainier* Mathis and Zack) that are presently known only from Mt. Rainier, along with several species exhibiting extremely limited northwest distributions. Further investigations of montane areas might provide several new species and help define the ranges of the several rarely encountered ones.

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Nitrogen Yield in Reproductive Organs of Crested Wheatgrass[1]

Abstract

Nitrogen yield of reproductive organs in crested wheatgrass (*Agropyron desertorum*) were, in 3 years, approximately 0.9, 2.4, and 3.0 kg/ha per annum and were associated with herbage yields of 298, 1636, and 1522 kg/ha, respectively. In 1 year, heavy rains shortly after anthesis caused increases in herbage yield and, despite a decline in herbage N concentration, no net decrease in absolute N in the aerial biomass occurred in the subsequent 6 weeks. In a year, with dry conditions prevailing after anthesis, a net loss of absolute N (5.5 kg/ha) occurred in the aerial portions in the following 5 weeks. Of that 5.5 kg, 3.0 kg/ha (55 percent) was accounted for by N contained in the reproductive organs.

Introduction

Westselaar and Farquhar (1980), after a comprehensive review of the world's literature, infer the absolute amount of N in the aerial biomass of plants peak near anthesis and subsequently decreases with time as the crop matures. They conclude, "For perennial species such losses are at least partially accounted for by accumulation in below-ground storage organs," and "Net losses from tops may result from cumulative effects of a large number of small losses, some of which increase with N content or with senescence." Quantitative estimates of the various N-loss compartments are needed when assessing nitrogen balance in the plant-soil system. This paper reports quantitative estimates of N in the reproductive organs of Nordan crested wheatgrass (*Agropyron desertorum*) and concomitant N yield change in herbage from anthesis to seed development.

Locale and Procedure

The study was conducted on a sandy loam soil located on the Squaw Butte Experiment Station, 68 km west of Burns, Oregon. Median precipitation amount for the period 1 September to 30 June is 25 cm. The months of July and August are usually dry (median precipitation is less than 0.4 and 0.6 cm, respectively). The 9 x 18 m plots selected were seeded in 1954 and revelant data collected in 1967, 1969, and 1978.

In 1967, 100 yield plots (.093 m^2) at random along rows 0.3 m apart were harvested on 29 June (onset of anthesis) and the numbers of reproductive stems counted in each. The number of spiklets/head was determined from 100 randomly selected heads and the number of florets/spiklet determined from a random sample of 30 stems. Twenty samples of reproductive organs, each containing 10 floral units (30 anthers plus filiments, style, plumules, and ovaries) were obtained with the aid

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of tweezers for N determination. An additional sample of anthers only was obtained by hand stripping the heads in the field.

In 1969, herbage yield plots (0.19 m^2) at random along rows 0.6 m apart were harvested on 13 June (anthesis onset), 1 July (anthesis termination), and 23 July (seed firm). Reproductive stems in all samples of the first two harvest dates were counted. Nitrogen concentration of 15 randomly selected yield samples for each harvest date was determined. Head length was measured to the nearest mm on nine reproductive heads selected at random on 13 June and N determined on the reproductive organs plucked from each seedhead.

Attempts to continue the study were made in a number of subsequent years, but precipitation following anthesis caused the author to abort the study. In 1978, a favorable dry sequence occurred and scheduled sampling was completed. In that year on 1 July when anthesis was noticed, 100 herbage yield plots (0.19 m^2) at random along rows 0.6 m apart were harvested, reproductive stems in each sample counted and oven dry weight and N concentration determined. The lengths of 25 seedheads selected at random were measured to the nearest mm and the reproductive organs removed and analyzed for N. An additional 350 seedheads collected at random were also measured for length. On 8 August terminal yield and N concentration were obtained.

Yield samples were oven dried at 50-60°C, weighed, and then processed in a Wiley mill for N analyses. Reproductive samples were air-dried prior to laboratory analyses and results reported on a dry weight basis. The Kjeldahl procedure used did not include special techniques to ensure total reduction of nitrate-N present. Data means within a year were tested with "t" at the 5 percent probability level.

Results and Discussion

Mean weight, numbers, and statistics for the various components in 1967 are presented in Table 1. The mean N yield in the reproductive organs from component estimates

TABLE 1. Seedhead components measured in crested wheatgrass, 29 June 1967.

Component	Measure	Sample size
Floral yield (grams/unit[1])	0.0042±0.0005[2]	20
Florets (number/spiklet)	2.69±0.01[2]	30
Spiklets (number/head)	15.61±1.32[2]	100
Heads (number/m^2)	150.4±11.7[2]	100

[1]Unit=30 anthers plus associated reproductive parts.
[2]P=0.05.

was 0.92±0.10 kg/ha at the 5 percent probability level. That amount was associated with a mean herbage yield of 928 kg/ha resulting from a September to June precipitation amount of 30 cm. Nitrogen concentration of anthers hand-stripped in the field (2.9 percent) was about 0.6 percent lower than contained in hand-plucked samples of all reproductive organs (3.5 percent).

The mean N concentration of reproductive organs was 4.2 percent in 1969 and the mean yield of nitrogen per head estimated at 0.88±0.4 mg at the 5 percent probability level. With 268 reproductive stems per m^2 (Table 2), the nitrogen yield of floral parts per hectare was estimated at 2.4 kg on 13 June. During the period 20 to 28

TABLE 2. Sampling estimates for crested wheatgrass in 1969.

Harvest date	Sample mean	Confidence interval[1]	Sample size
	Herbage yield (kg/ha)		
13 June	1340	± 24	100
1 July	1622	± 20	100
23 July	1711	± 26	100
13 June	1636	±381	15
1 July	1590	±456	15
23 July	2358	±647	15
	Reproductive stems (no/m^2)		
13 June	268	± 6	100
1 July	278	± 5	100
	Herbage nitrogen (%)		
13 June	1.01	± 0.04	15
1 July	.83	± 0.06	15
23 July	.71	± 0.07	15
	Herbage nitrogen yield (kg/ha)		
13 June	16.5	± 0.4	15
1 July	13.2	± 0.4	15
23 July	16.7	± 0.5	15

[1]P=0.05

June, 3.1 cm of precipitation occurred and caused a continuation of growth such that a herbage yield increase occurred between 13 June and 23 July (as judged by the 100 samples). Thus, despite a loss of reproductive organs and a decline in herbage N concentration from 1.01 to 0.83 to 0.71 percent following anthesis during the sampling period, there was no significant change in N yield in the aerial portions between 13 June and 23 July. The mean herbage yield (1636 kg/ha) on 13 June contained 16.5 kg of N including the 2.4 kg in the reproductive organs. During the September to 13 June period 24 cm of precipitation was received.

It is clear from Table 2 that use of 15 yield samples was insufficient to estimate the mean herbage yield with acceptable precision, although that number was adequate (as judged by the 95 percent confidence interval) to estimate mean nitrogen concentration. The nine seedheads from which reproductive organs were removed was only marginally acceptable.

Herbage yield on 1 July 1978 was 1522 and increased to 1611 kg/ha by 8 August, a nonsignificant increase (Table 3). Herbage nitrogen in the same period decreased significantly ($P<0.05$) from 0.93 to 0.54 percent. From these values, nitrogen yield in the aerial portions was estimated to be 14.2 kg/ha on 1 July and 8.7 kg/ha on 8 August, a net loss of 5.5 kg/ha (39 percent of that present on 1 July).

Data in 1969 suggested a linear relation between total nitrogen in the reproductive organs in seedheads with the length of the seedhead. But because of the small sample size and several sterile florets, the relation was not well expressed. In 1978, the mean N/hd was 1.467±0.38 mg based upon the 25 samples with a mean seedhead length of 52.8 mm. However, total N in the reproductive organs was significantly (<0.05) related ($r=0.85$) with head length (Fig. 1). The population mean seedhead length of 44.0 mm as estimated from the 350 samples and the regression relation suggest that the true mean N/hd is about 1.08 mg. Using 1.08 mg/hd and 275 reproductive stems per m^2, 3.0 kg/ha of N is estimated in that compartment of the aerial biomass. This

TABLE 3. Sample estimates for crested wheatgrass in 1978.

Harvest date	Sample mean	Confidence interval[1]	Sample size
	Herbage yield (kg/ha)		
1 July	1522	±182	100
8 August	1611	±140	100
	Herbage nitrogen (%)		
1 July	0.93	± 0.02	100
8 August	0.54	± 0.01	100
	Reproductive stems (no/^{2}m)		
1 July	275	± 8	100
	Seedhead length (mm)		
1 July	52.8	± 7.4	25
1 July	44.0	± 1.8	100

[1]P=0.05.

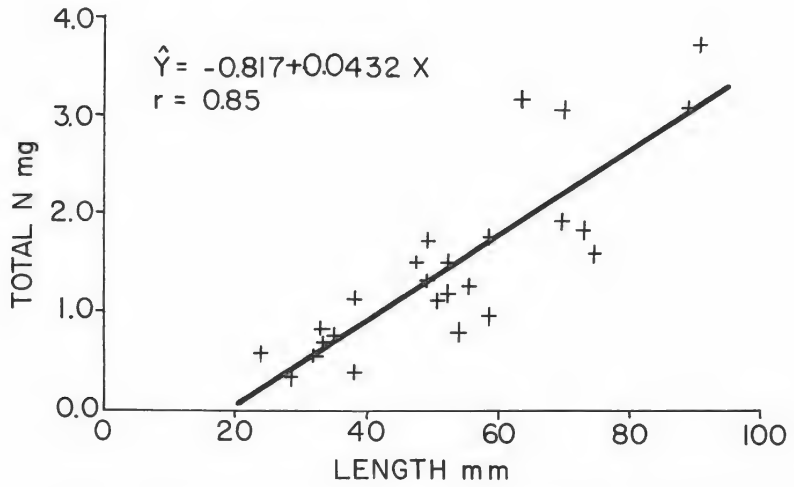

Figure 1. Total N in reproductive organs of crested wheatgrass as a function of seedhead length (1978).

estimate represents about 21 percent of the total N in the aerial portion on 1 July and is 55 percent of the nitrogen that disappeared from the aerial portion between 1 July and 8 August. During the September to June cropyear period, the total precipitation was 32 cm.

Precipitation occurring after anthesis may or may not significantly alter nitrogen contents in crested wheatgrass plants. However, if a sufficient amount of precipitation is received, as in 1969, nitrogen translocation may be delayed or confounded and the likelihood of large errors in sampling increased. Thus, the absence of precipitation following anthesis is more desirable to obtain a clear picture of the N yield-loss relation.

Plucking out the total reproductive unit probably overestimates the amount of N actually lost, as the ovary or a part of it is assimilated in the seed formation process. In contrast, plucking at the first visual observation of anthesis likely underestimates

the N lost as the yield of reproductive organs is perhaps reduced because of immaturity. Also, since the Kjeldahl procedure used did not reduce the nitrate-N component, total N is underestimated to that extent.

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Food Habits of the Shorthead Sculpin (Cottus confusus) in the Big Lost River, Idaho

Abstract

Feeding habits of the shorthead sculpin (*Cottus confusus*) were analyzed by size in both autumn and spring, and by habitat type in the spring. Indices of relative importance, fullness, and benthic electivity were developed. Trichoptera, Diptera, and Ephemeroptera larvae were the most important food items with some seasonal variation. *Paragyractis* sp. larvae (Lepidoptera) was important only in the spring. Larger sculpin cannabalized both smaller fish and eggs.

Introduction

The role of freshwater sculpin (*Cottus*) in "salmonid" streams has been receiving increasing attention, especially the cottid/salmonid food-habit interaction. Adverse effects of sculpin on trout and salmon populations by competition for food and/or by predation on eggs and fry has been suggested (Primbs and Platts 1976). Under unnatural conditions, such as aquaria studies and areas where salmonid fry are stocked in high densities, sculpin have taken advantage of this food source (Phillips and Claire 1966; Patten 1971a, 1971b; Clary 1972). Sculpin are known to prey primarily on benthic macroinvertebrates, while occasionally taking algae, detritus, and other fishes (Bailey 1952, Zarbock 1952, Northcote 1954, Daiber 1956, Ebert and Summerfelt 1969, Antonelli *et al.* 1972, Pasch and Lyford 1972, Novak and Estes 1974, Craig and Wells 1976, Li and Moyle 1976, Moyle 1977).

Little is known of the life history of the shorthead sculpin (*Cottus confusus*), since it only recently has been recognized as a distinct species (Bailey and Bond 1963, Scott and Crossman 1973). *C. confusus* distribution is also restricted to the Columbia River and Puget Sound drainages. The Big Lost River (Idaho) has been "isolated" from the Snake River by Pleistocene lava flows and now enters playas after traversing the Arco desert, flowing south underground to the Snake River (Andrews 1972, Overton 1977). The Big Lost supports an abundant population of shorthead sculpin, together with four salmonid species—rainbow trout (*Salmo gairdneri*), brook trout (*Salvelinus fontinalis*), mountain whitefish (*Prosopium williamsoni*), and sockeye salmon (*Oncorhynchus nerka*). The rainbow trout is the most abundant salmonid species in the

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study area (see Overton (1977) for a complete description of the fisheries). The purpose of this research was to determine food habit information on this little-known species. Additionally, this information may help to define the ecological role of sculpins in "salmonid" streams.

Methods and Materials

In autumn of 1976 (25 September and 2 and 3 October), 291 shorthead sculpin were collected by both AC and DC electrofishing gear from a 2-km reach immediately downstream from the Idaho National Engineering Laboratory (INEL) diversion dam without reference to habitat type; most fish were collected with the DC shocker. In the spring of 1977 (24 April), 184 sculpin were collected from three discrete habitat areas, a race, riffle, and a pool. The race area was located at the outfall of a 2 m-diameter corrugated steel culvert from which the water fell a distance of about 0.3 m to the stream bed of cobble-boulder substrate of interstitial sand and small gravel. The current here was swiftest of the three locations, with a water depth of 0.5-1.0 m and width of approximately 1.5 m. Water depth in the riffle area was 0.1-0.3 m over an embedded gravel-marl substrate; stream width was about 2.2-4 m. Current velocity here was intermediate to that of the other two locations. The pool substrate consisted of small pebbles interspersed with numerous large boulders; width was 2.5-4.5 m. Stream flows at the time of the spring collection were low, approximately 2.5 cfs, as a result of drought conditions upstream from the INEL boundary.

All fish were placed in 10 percent formalin at the time of capture. Sex, weight to the nearest 0.1 g, and standard length to the nearest 1 mm were determined in the lab. Sixty fish, 15 each from four size groupings, were selected from the 291 sculpin autumn sample. The size groupings were: 24-40 (age class 1), 41-60 (classes 2 and 3), 61-74 (class 4), and 75-97 mm(classes 5 and 6) standard length (Gasser *et al* 1981). Stomachs were removed by severing the anterior esophagus and posterior intestine, and placed in separate vials of 40 percent isopropyl alcohol. Contents from only the stomach proper were removed for identification to the lowest taxa possible and counted. Reconstituted volumes of food items were obtained by alcohol displacement of a known number of a given food item. Organisms collected in spring kick samples were used for both spring and autumn calculations. In cases where organisms were too few to obtain volumes, estimates based on other organisms were used. The volumes of Chironomidae, *Omphiogomphus* sp. (Anisoptera), *Baetis* sp. (Ephemeroptera), and *Hydropsyche* sp. (Trichoptera), were representative of Simulidae, Coleoptera, and Plecoptera, *Paraleptophlebia* sp. (Ephemeroptera), and Rhyacophilidae (Trichoptera), respectively. Volumes for sculpin consumed as food items were taken as the volume of a 40 mm fish, since this was the size of the only fish recovered from stomach contents in measurable condition.

Percent composition of organisms in the benthic samples and in stomach content was calculated by number and by volume. Ivlev's electivity index was calculated for each benthic food item as :EI=R–P/R+P, where R is the percent composition of an organism in the gut contents, and P the percent composition of that same organism in the benthos (Powers 1974, Kilambi and Barger 1975). Drift samples of potential food items were not taken; the electivity indices are based entirely on the relative environmental abundance of benthic organisms determined from kick samples in each of the

three habitat types. An index of relative importance for each food item was calculated as: IRI=FO(N+V), where FO, N, and V are the numerical percentages of the frequency occurrence, number, and volume of the given food item in the gut contents, respectively (Talen 1976). The percent frequency occurrence of a food item was calculated as percent FO=(the number of stomachs containing the item/the number of stomachs containing food) $\times$ 100 percent (Novak and Estes 1974).

In order to assess the feeding intensity of sculpin, a "degree of fullness" status was assigned to each stomach by inspection based on its degree of distention. Stomachs were assigned to one of five categories: empty, nearly empty, nearly full, full, and very full.

Results and Discussion

Sculpin fed on a variety of aquatic insect larvae and other sculpin (Tables 1 and 2).

TABLE 1. Percent composition (by number and by volume) of stomach contents of **Cottus confusus** in the Big Lost River, Idaho, sampled Autumn 1976.

No. stomachs w/food = 49
Mean SL (mm) = 61.6

Food item	% number	% volume
Diptera		
Chironomidae	3.2	0.1
Simulidae	9.8	0.5
Tipulidae (**Hexatoma** sp.)	1.0	1.0
Ephemeroptera		
Baetis tricaudatus	26.0	1.3
Trichoptera		
Hydropsyche sp.	35.6	7.5
Leptoceridae and Limnephilidae	6.3	0.4
Rhyacophilidae	7.9	1.7
Anisoptera		
Omphiogomphus sp.	0.3	0.2
Hemiptera		
Notonecta sp.	5.4	3.1
Plecoptera		
Isogenus sp. and **Isoperla** sp.	3.5	2.0
Pisces		
C. confusus	1.0	82.1
Total number, volume (ml)	315	6.8

The variety of organism in the sculpin diet was greater in spring than in autumn, *Hydropsyche* (35.6 percent) was the most abundant food item, followed by *Baetis* (26.0 percent), other trichopterans (14.2 percent), and simulids (9.8 percent). Low autumn food consumption accounts for the high percentage (82.1 percent) of the volume represented by just three sculpin consumed by three of the 49 sculpin containing food. This volume value of sculpin exaggerates their importance as food items to the total sculpin population. *Hydropsyche*, which was the major contributor numerically, comprised only 7.5 percent of the volume.

Available benthos (kick samples) was compared with sculpin stomach contents from the three habitats sampled in spring (Table 2). The number of sculpin collected was 26, 65, and 93 for race, riffle, and pool, respectively. *Hydropsyche* comprised a substantial part of both the benthos and stomach contents. *Baetis*, which contributed significantly to the benthic samples, was insignificant as a food item. *Heptagenia* was

also an insignificant food item, but to a lesser extent. Chironomidae was found more commonly in the stomach contents than in the benthos at all three habitats; in the race habitat, chironomids comprised 1.7 percent of the benthic sample and 49.1 percent of the stomach contents. Pool-dwelling fish were the most active feeders; although fish were most abundant food, consumption per fish was greatest in the pool (Table 2).

TABLE 2. Percent composition by number and volume (ml) of food items in the stomach contents of **Cottus confusus** and in the benthos (in parentheses) of the Big Lost River, Idaho, sampled 24 April 1977.

Habitat:	Race		Riffle		Pool	
Food item	No.	Vol.	No.	Vol.	No.	Vol.
Diptera						
Chironomidae	49.1	5.7	12.6	2.1	17.1	1.3
	(1.7)	(0.3)	(9.6)	(2.1)	(7.9)	(2.2)
Simulidae	—	—	0.7	0.1	0.1	0.1
	(2.0)	(0.4)	(1.4)	(0.3)	(0.6)	(0.2)
Tipulidae	0.3	0.7	0.6	2.4	—	—
(**Hexatoma** sp.)	(0.4)	(1.8)	(0.2)	(0.8)	(0.2)	(1.5)
Empididae	—	—	—	—	0.1	0.1
	—	—	(0.4)	—	(0.4)	(0.1)
Ephemeroptera						
Baetis tricaudatus	1.2	0.1	2.5	0.5	1.1	0.9
	(27.9)	(5.5)	(22.5)	(5.4)	(18.0)	(5.4)
Heptagenia sp.	—	—	1.0	0.2	0.7	0.1
	(4.9)	(1.1)	(9.4)	(2.7)	(4.1)	(1.5)
Paraleptophlebia sp.	—	—	0.2	0.1	—	—
	—	—	(0.1)	(0.1)	—	—
Tricorythodes sp.	0.8	0.1	0.9	0.1	4.0	19.8
	(0.1)	(0.1)	(2.6)	(0.2)	(36.2)	(30.7)
Trichoptera						
Hydropsyche sp.	37.1	19.8	62.7	47.7	58.8	19.8
	(52.8)	(43.6)	(44.5)	(44.6)	(24.4)	(30.7)
Leptoceridae and	—	—	0.2	0.1	0.7	0.1
Limnephilidae	(0.4)	(0.1)	(1.5)	(0.5)	(2.5)	—
Anisoptera						
Omphiogomphus sp.	—	—	0.5	0.9	0.2	0.2
	(0.1)	(0.1)	(0.2)	(0.5)	(0.8)	(2.7)
Coleoptera						
unidentified	—	—	0.1	0.2	0.1	0.1
	(0.9)	(2.0)	(0.7)	(2.0)	(1.2)	(4.0)
Plecoptera						
Isogenus sp. and	0.8	1.1	2.1	4.3	0.7	0.6
Isoperla sp.	(5.5)	(12.4)	(4.8)	(13.1)	(0.8)	(2.7)
Lepidoptera						
Paragyractis sp.	10.4	72.4	15.8	41.3	14.9	65.6
	(3.0)	(32.7)	(2.1)	(27.9)	(2.8)	(45.2)
Pisces						
Cottus confusus	—	—	—	—	0.1	10.7
	—	—	—	—	—	—
Fish eggs (**C. confusus**)	0.3	0.1	0.1	0.1	2.1	0.6
	—	—	—	—	—	—
Total organisms	385	3.3	1106	6.7	2591	35.1
	(2603)	(14.5)	(2629)	(12.0)	(1269)	(4.6)

Habitat:	Race	Riffle	Pool
No. stomachs w/food	25	65	90
No. fish/size group*	(7,16,2,0)	(32,30,3,0)	(25,33,15,17)
Mean SL (mm)	47	42	56

*Numbers of fish (containing food) in each of the following size groups (SL in mm): 25-40, 41-60, 61-74, 75-91.

TABLE 3. Index of relative importance and electivity for benthos (in parentheses) of food items of **Cottus confusus** from three different habitats of the Big Lost River, Idaho, sampled 24 April 1977.

Habitat:	Race			Riffle			Pool			
Fish size (SL in mm): Food item	25-40	41-60	61-74	25-40	41-60	61-74	25-40	41-60	61-74	75-97
Diptera										
Chironomidae	3517 (+.93)	6388 (+.95)	390 (+.39)	581 (+.20)	705 (+.15)	43 (-.78)	1986 (+.54)	2323 (+.54)	549 (+.09)	446 (-.09)
Simulidae	—	—	—	41 (+.14)	1 (-.88)	—	2 (-.20)	1 (-.71)	—	—
Tipulidae (**Hexatoma** sp.)	200 (+.86)	—	—	45 (+.71)	5 (+.20)	83 (+.71)	—	—	—	—
Empididae	—	—	—	—	—	—	—	—	—	—
Ephemeroptera										
Baetis tricaudatus	—	23 (-.90)	—	120 (-.67)	53 (-.85)	43 (-.90)	35 (-.80)	52 (-.83)	18 (-.91)	1 (-.99)
Heptagenia sp.	—	—	—	16 (-.72)	17 (-.82)	—	35 (-.34)	11 (-.74)	5 (-.74)	6 (-.78)
Paraleptophlebia sp.	—	—	—	1	1	—	—	—	—	—
Tricorythodes sp.	200 (+.88)	—	—	15 (-.37)	15 (-.48)	—	966 (-.39)	246 (-.73)	12 (-.97)	—
Trichoptera										
Hydropsyche sp.	5426 (-.18)	4652 (-.98)	8350 (+.12)	8050 (+.13)	7974 (+.19)	7810 (+.18)	4674 (+.19)	7210 (+.35)	10540 (+.51)	8210 (+.46)
Leptoceridae and Limnephilidae	—	—	—	—	1 (-.67)	—	7 (-.98)	2 (-.79)	37 (-.10)	29 (-.43)
Anisoptera										
Omphiogomphus sp.	—	—	—	2 (-.20)	9 (+.50)	—	—	4 (-.70)	—	19 (-.23)
Coleoptera										
unidentified	—	—	—	—	1 (-.75)	—	—	1 (-.78)	—	7 (+.60)
Plecoptera										
Isogenus sp. and **Isoperla** sp.	122 (-.43)	30 (-.96)	—	288 (+.04)	30 (-.68)	127 (-.33)	84 (+.43)	18 (-.14)	12 (-.33)	24 (-.14)
Lepidoptera										
Paragyractis sp.	465 (-.15)	4769 (+.08)	11240 (+.81)	5006 (+.72)	6819 (+.76)	11300 (+.87)	6392 (+.68)	6499 (+.67)	6032 (+.59)	5776 (+.74)
Pisces										
C. confusus	—	—	—	—	—	—	—	—	—	299
Fish eggs (**C. confusus**)	—	4	—	—	11	—	—	—	117	106
No. stomachs w/food	7	16	2	32	30	3	25	33	15	17

Paragyractis was relatively abundant in stomachs from all habitats (Table 3). Volumetrically, *Paragyractis* was more important as a food item than it was numerically, comprising a substantial portion of the benthic samples and dominating the stomach contents in the spring, although not sampled in autumn (Table 4). *C. confusus* as a food item comprised 10.7 percent of the stomach content volume in the pool habitat. The larger sculpin, congregated in the pool area, were the only ones found to exhibit piscivory. Their consumption of other sculpin may be associated with their larger size and/or spawning activity.

Chironomids, which were abundant, were not important volumetrically (Table 2). Chironomidae made its greatest volumetric contribution (5.7 percent) to the stomach contents of fish in the race habitat. This "high" contribution of Chironomidae probably resulted from the small size (25-60 mm) of the sculpin collected in this habitat. These small organisms were strongly represented in the diet of the smaller fish in the spring, but not in autumn (Tables 3 and 4). Decreasing benthic electivity for chironomids with increasing fish size reveals a direct relationship between predator and prey size. *Tricorythodes* was also relatively abundant in the smallest fish in the race habitat; other-

TABLE 4. Index of relative importance of food items of **Cottus confusus** in the Big Lost River, Idaho, sampled Autumn 1976.

Fish size (SL in mm) / Food item	25-40	41-60	61-74	75-97
Diptera				
Chironomidae	183	13	11	45
Simulidae	1049	423	67	0
Tipulidae (**Hexatoma** sp.)	70	65	55	0
Ephemeroptera				
Baetis tricaudatus	3924	1635	583	792
Trichoptera				
Hydropsyche sp.	6400	5689	6990	3940
Leptoceridae and Limnephilidae	68	293	542	23
Rhyacophilidae	238	505	939	0
Anisoptera				
Omphiogomphus sp.	0	0	0	24
Hemiptera				
Notonecta sp.	0	503	167	293
Plecoptera				
Isogenus sp. and **Isoperla** sp.	492	355	536	0
Pisces				
C. confusus	0	0	0	2635
No. stomachs w/food	13	12	12	12

wise, it was uncommon to scarce in the diet. *Heptagenia* was considerably less abundant in the diet than the benthos (Tables 2 and 3). Ivlev's electivity indices may range from –1, indicating that the item is found in the environment but not in the stomach contents, to +1 when the converse is true. Novak and Estes (1974) reported forage ratios greater than one for *Baetis* (1.5) and Chironomidae (2.5) consumed by *Cottus baileyi* from July to October in Virginia. Those fish ranged from 20-70 mm SL; *C. confusus* of similar size had relatively more chironomids than did *C. baileyi. C. baileyi* contained few *Hydropsyche* (0.2), whereas in most cases *C. confusus* contained a slightly greater percentage than the benthos.

Hydropsyche, which was generally the most abundant aquatic insect in the environ-

ment, was moderately accumulated by the larger fish (60 mm) in the race habitat. Although most abundant in the race, it was less abundant in the diet of the smaller sculpin; even though not selected for their availability, a high IRI results. This observation was also true for *Paragyractis* (Table 3). Pit sculpin (*Cottus pitensis*) also consumed *Hydropsyche* in proportion to the abundance of the insect in the environment (Li and Moyle 1976). *Paragyractis* was also only accumulated by the larger fish in the race habitat. *Paragyractis* was also common in pit sculpin during the spring and summer months in California. The abundance of *Paragyractis* in the *C. confusus* diet reflects the substantial volume and relative food value of *Paragyractis* (Table 3).

The index of relative importance facilitates recognition of the value of the food items to the consumer; this index compensates for disproportionate number and/or volume estimates which, when used alone, misrepresent the value of food items to the population. Volume estimates of sculpin as food items represent one such instance (Table 1). The index may range from zero to 20,000, indicating no utilization and maximum possible utilization, respectively (Tables 3, 4, 5). The importance of *Hydropsyche* to all fish is obvious: *Paragyractis* was most important to sculpin in the 61-74 mm size category in the race and riffle areas, and least important to the smaller fish in the race habitat.

Baetis was consistently more important to smaller fish (25-60 mm) than to larger fish. *Baetis*, second in overall importance to sculpin of all sizes in autumn, was considerably less important in the spring. This finding may be explained by the relative unavailability of other food items during the autumn, since *Baetis* was uncommon in the diet despite its abundance in the spring (Tables 2, 3, 4). Simulids played an important role in the diet of small sculpin in autumn but not in spring, when chironomids were most important. This observation may reflect seasonal changes in the relative abundance of chironomids. Pasch and Lyford (1972) noticed an increased environmental abundance of simulids accompanied by an increased utilization by *Cottus rhotheus* in Oregon. *Trichorythodes*, found only in spring sculpin, was fairly important to the smallest fish (25-40 mm), but not utilized by sculpin larger than 74 mm. *Tricorythodes* was most important to fish in the pool habitat where it was also most abundant, yet it was least selected for in this area (Tables 3 and 4). The high selection value for *Tricorythodes* in the race may be fortuitous, however, since its benthic occurrence there is so slight (0.1 percent) that any consumption of this organism would necessarily yield a high electivity index.

These data substantiate the direct relationship between predator and prey size (Northcote 1954, Daiber 1956). Northcote, working with *Cottus asper* and *C. rhotheus* in British Columbia, found that smaller organisms (plankton and chironomids) were more important to the fry of both species than to the adult fish. Larger food items, chiefly ephemeropteran nymphs, were important to the larger fish (30-69 mm total length). Fish, *Richardsonius balteatus* and *Ptychocheilus oregonense*, were predominant food items of sculpin larger than 69 mm total length. Similar feeding relationships were exhibited by *Cottus bairdi bairdi* in a small headwater stream in New York (Daiber 1956). Partitioning of food resources between *C. rhotheus* and *Cottus perplexus* was also based on differences in their maximum size. *C. perplexus*, with its smaller size and proportionately smaller mouth, was restricted to smaller food items (midge larvae and baetid nymphs) than was *C. rhotheus* (Pasch and Lyford 1972). When fish size is

disregarded, *Hydropsyche* is still the mainstay of the sculpin diet (Table 5). Simulids, baetids, other trichopterans, and fish were more important in autumn than in spring. Conversely, Chironomidae and *Paragyractis* were more important in spring than in autumn.

Sculpin larger than 40 mm SL fed about twice as heavily in spring than they did in autumn, as indicated by comparison of percentages of stomachs in the "full" categories (Table 6). The spring increase in consumption by *C. confusus* is reflected by an increase

TABLE 5. Index of relative importance of food items of **Cottus confusus** in the Big Lost River, Idaho, sampled Autumn 1976 and Spring 1977.

	Autumn 1976	Spring 1977		
Habitat:	Variable	Race	Riffle	Pool
Food item				
Diptera				
Chironomidae	40	4384	634	1288
Simulidae	295	0	9	1
Tipulidae (**Hexatoma** sp.)	12	4	32	0
Empididae	0	0	0	1
Ephemeroptera				
Baetis tricaudatus	1450	10	79	38
Heptagenia sp.	0	0	15	11
Paraleptophlebia sp	0	0	1	0
Tricorythodes sp.	0	7	13	146
Trichoptera				
Hydropsyche sp.	3607	5007	10532	7687
Leptoceridae and Limnephilidae	150	0	1	1
Rhyacophilidae	196	0	0	0
Anisoptera				
Omphiogomphus sp.	1	0	11	2
Coleoptera				
Unidentified	0	0	1	1
Hemiptera				
Notonecta sp.	104	0	0	0
Plecoptera				
Isogenus sp. and **Isoperla** sp.	112	23	57	23
Lepidoptera				
Paragyractis sp.	0	4306	4043	5901
Pisces				
C. confusus	507	0	0	24
Fish eggs (**C. confusus**)	0	2	1	21
No. stomachs w/food	49	25	65	90
No. fish/size group*	(13,12,12,12)	(7,16,2,0)	(32,30,3,0)	(25,33,15,17)
Mean SL (mm)	61.6	46.8	42.4	55.7

*Numbers in parentheses indicate the number of fish containing food in each of the following size groups (SL in mm): 25-40, 41-60,61-74, 75-97.

in condition ($\frac{W}{L^3} \times 10^5$) of spring fish over those in autumn (Gasser *et al.* 1978).

Ebert and Summerfelt (1969) also reported higher consumption levels in spring and summer than in autumn and winter for Piute sculpin (*Cottus beldingii*) in Lake Tahoe, California.

Cottids are primarily opportunistic feeders whose diets consist of aquatic insect larvae, though fish occasionally are important. The diet of *C. beldingii* included green fila-

TABLE 6. Index of fullness for **Cottus confusus** in the Big Lost River, Idaho, sampled Autumn 1976 and Spring 1977.

Fish size (SL in mm):	25-40	41-60	61-74	75-97
Autumn 1976: No. stomachs examined	15	15	15	15
Percent empty	13	20	20	20
Percent nearly empty	7	33	27	40
Percent nearly full	20	13	13	13
Percent full	33	20	27	7
Percent very full	27	13	13	20
Spring 1977: No. stomachs examined	65	81	21	17
Percent empty	2	2	5	0
Percent nearly empty	20	7	10	12
Percent nearly full	32	20	19	12
Percent full	25	31	33	23
Percent very full	21	40	33	53

mentous algae, chironomids, plecopterans, amphipods, cladocerans, moss capsules, and oligochaetes; diet varied with fish size, season, depth of capture, and collection date (Ebert and Summerfelt 1969). Dipterans, ephemeropterans, plecopterans, coleopterans, and oligochaetes were most important in the diet of *C. tenuis*, though chironomids were selectively consumed (Antonelli *et al.* 1972). Chironomidae was the dominant food item of *Cottus cognatus* from Alaska, but they also consumed other dipterans, ephemeropterans, and plecopterans (Craig and Wells 1976). Likewise, *Cottus pitensis* in California subsisted on dipteran, ephemeropteran, trichopteran, plecopteran, lepidopteran, and other insect larvae, with selection for *Paragyractis* and Baetidae. Although *C. pitensis* occasionally consumed other sculpin, none were found in the stomach contents of over 300 sculpin collected during the months of May, June, and October (Li and Moyle 1976). The food habits of *C. confusus* in the Big Lost River closely parallel those of other cottids.

Bottom-dwelling aquatic insects comprised 99.7 percent of the diet of *Cottus bairdii punctulatus* in Montana (Bailey 1952). Chironomid and trichopteran larvae accounted for 56 percent and 37 percent, respectively, of the total number of organisms consumed. Only one sculpin (*C. b. punctulatus*), one dace (*Rhinichthys cataractae*), and seven cottid eggs were found in the gut contents of 768 *C. b. punctulatus* collected over a 20-month period. Dipterans, plecopterans, ephemeropterans, and trichopterans, in order of decreasing importance, were principal food items of *Cottus bairdi semiscaber* in Utah (Zarbock 1952). Two sculpin, two muddler eggs, and three trout eggs were found in the 275 fish collected over a nine-month period. Ten sculpin were taken from the gut contents of 307 *C. b. bairdi* collected over an eight-month period (Daiber 1956). Food items of 27 *C. perplexus* and 48 *C. rhotheus* included two sculpin and 19 cottid eggs (Pasch and Lyford 1972). In this study, five of the 229 *C. confusus* examined had each consumed one sculpin, whereas nine sculpin consumed a total of 56 sculpin eggs. The resulting low IRI confirm that the degree of piscivory exhibited by *Cottus* is slight.

Potential effects of cottids on salmonid populations via competition or direct predation on salmonid eggs and/or fry have been investigated (Patten 1962, 1971a, 1971b; Reed 1967). The ecological interactions between cottids and salmonids are not yet well defined, but the longevity of the association—about 3 million years (Linder 1970 and pers. comm.)—strongly suggests ecological compatibility between the two. Ricker

(1941) documented the occurrence of sculpin in the diets of char and trout in Cultus Lake, British Columbia. Ricker also noted that sculpin, as well as char, coho salmon, mountain whitefish, and sockeye salmon, consumed sockeye fry, although the number of sockeye migrants remained constant between 1932 and 1933 lakeward migrations. Reed (1967) considered sculpin the major predator of chum salmon eggs; however, the effect of this predation on salmon populations over time was not considered. Cottid predation on coho salmon fry has been described as incidental and insignificant (Patten 1962). Cottids may be significant food items for salmonids; they comprised 45 percent by number and 38 percent by volume of stomach contents of young-of-the-year sockeye salmon in Brooks Lake, Alaska (Heard 1965). The development of cottid/salmonid interaction is probably of benefit to both groups.

The fact that cottids and salmonids are ecologically segregated on the basis of feeding habits has been demonstrated. The bottom-feeding habits of sculpin complement the drift and surface-feeding modes of trout and salmon (Dineen 1951, Zarbock 1952, Brocksen *et al.* 1968, Antonelli *et al.* 1972, Craig and Wells 1976, Li and Moyle 1976). *C. confusus* appears to conform to the bottom feeding pattern of other sculpin.

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A Mathematical Model of the Paradox of Enrichment in Arthropods: Comparison between Theory and Experiment

Abstract

The paradox of enrichment refers to a situation in which an originally stable predator-prey ecosystem is destabilized by tripling the food supply available to the herbivore, resulting in the extinction of both species due to overexploitation. An existing arthropod predator-prey model incorporating age structure in the carnivore is extended to include the effects of intraspecific carnivore competition. A linear stability analysis of the community equilibrium point of that differential-integral equation system is performed and the results are compared to those obtained by employing an analogous differential equation model without age structure. It is shown that, unlike for the latter model, the paradox of enrichment can now occur even for a carnivore which exhibits intraspecific carnivore competition. This prediction is in accordance with relevant experimental evidence involving mites on oranges.

Introduction

The *paradox of enrichment* is a term coined by University of Arizona ecologist M. L. Rosenzweig (1971) to describe the outcome of a laboratory experiment involving two mite species conducted by a team of Berkeley entomologists under the direction of C. B. Huffaker. The ecosystem under examination consisted of the herbivorous six-spotted spider mite *Eotetranychus sexmaculatus* Riley feeding on oranges while, in turn, being preyed upon by the carnivorous mite *Metaseiulus occidentalis* Nesbitt in a controlled environment of carefully constructed cabinets. Huffaker *et al.* (1963) observed that for universes composed of a particular fixed amount of oranges the population densities of the two mite species per cabinet tended to persist in ecological time. Then they were able to destabilize this originally stable situation by tripling the food supply available to the herbivorous mite, which resulted in the extinction of both mite species due to overexploitation. In what follows we shall survey two attempts to model this phenomenon mathematically.

The Differential Equation Model

Rosenzweig (1971) modeled this two-species ecosystem by introducing two differentiable functions, $H(t)$ and $C(t)$, which represented the population densities of herbivores (the prey) and carnivores (the predators) at time, t. Assuming the occurrence of overlapping generations, he posed a series of differential equation models to describe the sizes of these populations. For our purposes it suffices to consider the generic system

$$\frac{dH}{dt} = r(H)H - Cf(H) = F(H,C) \tag{1a}$$

and

$$\frac{dC}{dt} = -C + r_2 g(H,C)C = G(H,C) \tag{1b}$$

which preserves the essential features of Rosenzweig's analysis. Here $r(H)$ is the intrinsic per capita growth rate of prey when no predators are present, $f(H)$ is the *functional response* of the predator—i.e., the density of prey killed per unit time by a single average predator, r_2 is the maximum per capita intrinsic growth rate of the predator with an unlimited food supply, and $g(H,C)$ represents the conversion of prey consumed into predator births. Implicit to the formulation of this system is the requirement that these populations must be relatively numerous and distributed uniformly in space. Note that in (1a) and (1b) we have chosen the time scale so that the lifetime of the predator is one unit—i.e., one unit of time $\equiv$ 16 days.

There exists a critical point (H_0,C_0) of the system of (1)—i.e., a steady state solution

$$H(t) = H_0 \text{ and } C(t) = C_0, \tag{2a}$$

satisfying

$$F(H_0,C_0) = 0 \text{ and } G(H_0,C_0) = 0, \tag{2b}$$

which represents a community equilibrium point provided

$$H_0 = g^{-1}(1/r_2) > 0 \text{ and } C_0 = r(H_0)H_0/f(H_0) > 0 \tag{2c}$$

where

$$g^{-1} \text{ is the inverse function of } g(H) \equiv g(H,C_0).$$

Although there exist critical points of our system containing zero components, that type of equilibrium where both species are present is the one of primary biological interest within the context of the experiments of Huffaker *et al.* One of the simpler ways to represent the community equilibrium point of (2) graphically is to plot the *isoclines* of system (1) simultaneously on a two-dimensional graph in the H-C plane (Rosenweig and MacArthur 1963). The herbivore isocline is the locus of those H and C that satisfy the condition

$$F(H,C) = 0 \tag{3a}$$

while the carnivore isocline satisfies the companion condition

$$G(H,C) = 0. \tag{3b}$$

The point of intersection of these two curves represents the community equilibrium point as depicted in Figure 1a. Although the functions contained in F and G need only have a generic form that yields isoclines of the shape indicated in that figure, there is also some merit in offering an explicit representation. Toward that end we take $r(H)$, $f(H)$, and $g(H,C)$ of the form

$$r(H) = r_1(1 - H/K), f(H) = aH/(H + b_1), \text{ and}$$
$$g(H,C) = H/(H + b_2 + b_3C^2) \tag{4a}$$

where

$$r_1,K,a > 0,\ 0 < b_1 < K, \text{ and } 0 < b_2 < (r_2 - 1)K \text{ for } r_2 > 1. \tag{4b}$$

In order to determine conditions under which there can exist a *stable* community equilibrium point for this system, we first perform a *linear* perturbation analysis of the critical point of (2). Thus we consider a solution of system (1) of the form

$$H(t) = H_0 + x(t),\ C(t) = C_0 + y(t) \tag{5a}$$

where

$$|x| << H_0 \text{ and } |y| << C_0. \tag{5b}$$

Substituting (5) into the basic equations of (1), expanding F and G in Taylor series about $H = H_0$ and $C = C_0$, making use of (2b), and neglecting all nonlinear terms in

the perturbation quantities $x(t)$ and $y(t)$, we obtain the following set of perturbation equations.

$$\frac{dx}{dt} = F_1(H_0,C_0)x + F_2(H_0,C_0)y \tag{6a}$$

and

$$\frac{dy}{dt} = G_1(H_0,C_0)x + G_2(H_0,C_0)y, \tag{6b}$$

where partial derivatives with respect to H and C have been designated by subscripts "1" and "2", respectively. Implicit to a predator-prey interaction, or more generally to any *exploitation* interaction, are the inequalities $F_2(H,C) < 0$ and $G_1(H,C) > 0$. The prey isocline of (3a), $F(H,C) = 0$, can be solved for $C = P(H)$ to obtain $F[H,P(H)] = 0$. Differentiating this with respect to H and evaluating the resultant condition at equilibrium yields the following form for the prey perturbation equation

$$\frac{dx}{dt} = \alpha(k_1 x - y), \tag{7a}$$

where $\alpha = -F_2(H_0,C_0) > 0$ and $k_1 = P'(H_0)$. Similarly the predator isocline of (3b), $G(H,C) = 0$, can be solved for $H = V(C)$ and then proceeding in an identical manner to that outlined above, the predator perturbation equation becomes

$$\frac{dy}{dt} = \beta(x - k_2 y) \tag{7b}$$

where $\beta = G_2(H_0,C_0) > 0$ and $k_2 = V'(C_0)$.

We now look for solutions of (7) of the form

$$[x,y](t) = [A,B]e^{\lambda t} \tag{8}$$

where λ is the growth rate of the perturbation quantities, while A and B are constants which could be determined given initial valves for the perturbations. Substituting (8) into (7), we obtain two linear homogeneous equations in the two constants A and B. If this *eigenvalue* system for λ is to have a nontrivial solution for the eigenvector components A and B, then the determinant of their coefficients must vanish. That requirement

$$\begin{vmatrix} \alpha k_1 - \lambda & -\alpha \\ \beta & -(\beta k_2 + \lambda) \end{vmatrix} = 0$$

yields the following so-called secular equation for λ:

$$\lambda^2 + (\beta k_2 - \alpha k_1)\lambda + \alpha\beta(1 - k_2 k_1) = 0. \tag{9}$$

An interpretation of the parameters appearing in the above secular equation seems appropriate at this point. The exploitation parameters α and β are a measure of the strength of the *interspecific* interactions at equilibrium, while k_1 and k_2 are related to the slopes of the isoclines at equilibrium and hence involve *intraspecific* interactions for the prey and predator, respectively. Intraspecific herbivore competition occurs when $k_1 < 0$ and herbivore mutualism, or cooperation, when $k_1 > 0$. For $k_2 > 0$ intraspecific carnivore competition results, while $k_2 < 0$ corresponds to carnivore mutualism. Should $k_2 = 0$, there is no intraspecific carnivore interaction. In particular for the functions defined in (4), the corresponding prey and predator isoclines are given by

$$C = P(H) = \frac{r_1}{a}(H + b_1)(1 - H/K) \quad \text{for } 0 \leq H \leq K \tag{10a}$$

and

$$H = V(C) = \frac{b_2 + b_3 C^2}{r_2 - 1} \quad \text{for } C \geq 0, \tag{10b}$$

respectively. We note that when $b_3 = 0$, the predator isocline reduces to the line —i.e., no intraspecific carnivore interaction—originally treated by Rosenzweig (1971). For intraspecific carnivore competition, $b_3 > 0$. Viewing H as the independent variable $H \equiv b_2/(r_2 - 1) < K$. Hence $k_2 \equiv 0$ and this is the case of nonsquabbling predators for both isoclines, k_1 and $1/k_2$ represent the slopes of the prey and predator isoclines, respectively, at equilibrium in Figure 1a. That is, the predator isocline of (10b) would be given by

$$C = \left[\frac{(r_2 - 1)H - b_2}{b_3}\right]^{1/2} \quad \text{for } H \geq b_2/(r_2 - 1). \tag{10c}$$

Since

$$\lim_{t \to \infty} |e^{\lambda t}| = \lim_{t \to \infty} e^{(Re\lambda)t} = \begin{cases} 0 & Re\lambda < 0 \\ 1 & Re\lambda = 0 \\ \infty & Re\lambda > 0 \end{cases}, \tag{11}$$

we say that the stability behavior of the solution of (1), given by the critical point of (2), to perturbations of the type of (5) and (8) depends upon the sign of $Re\lambda$ with stability occurring when $Re\lambda < 0$ for all λ satisfying (9). Equation (9) is of the form

$$\lambda^2 + b\lambda + c = 0 \tag{12a}$$

with

$$b = \beta k_2 - \alpha k_1 \quad \text{and} \quad c = \alpha\beta(1 - k_2 k_1). \tag{12b}$$

Noting that such quadratics have roots λ satisfying $Re\lambda < 0$ if and only if (Uspensky 1948)

$$b > 0 \quad \text{and} \quad c > 0, \tag{12c}$$

we have stability for those k_2 and k_1 such that

$$k_1 < \frac{\beta}{\alpha} k_2 \quad \text{and} \quad k_1 k_2 < 1 \tag{13}$$

since $\alpha,\beta > 0$. This region can be represented graphically in the $k_2 - k_1$ plane as in Figure 1b which has been drawn for $\alpha = \beta = 4.5$.

Rosenzweig (1971) considered exploitation in a two species ecosystem with a vertical predator isocline ($k_2 \equiv 0$) and with the prey limited by their environment to a finite carrying capacity, K, which was an increasing function of their food supply. Observe from (13) or from an examination of the k_1 axis in Figure 1b that when $k_2 \equiv 0$ ($b_3 = 0$) there will be local stability of the community eqlilibrium point provided

$$k_1 < 0. \tag{14}$$

Given the stability criterion of (14), Rosenzweig concluded that a predator-prey system which originally had a prey carrying capacity K_1 corresponding to a $k_1 < 0$ could be destabilized by enriching the food source of the prey sufficiently so that the new carrying capacity K_2 would correspond to a $k_1 > 0$ (see the vertical $b_3 = 0$ isocline of Fig. 1a). Since the predator density at equilibrium increased as the system was enriched while the prey density *remained the same* by virtue of the vertical predator isocline, Rosenzweig (1971) conjectured that the predator was relatively too numerous for the prey at equilibrium for the system to persist. However, for intraspecific carnivore interaction of a competitive nature ($k_2 > 0$), Rosenzweig (1972) found that enrichment inevitably resulted in a new stable ($k_1 < 0$) community equilibrium point with higher population density levels for both species (see the $b_3 > 0$ isocline of Fig. 1a), since the fourth quadrant of the $k_2 - k_1$ plane lies entirely within the stability region of Figure 1b.

The Age Structure Model

As has just been demonstrated, the paradox of enrichment can occur for a differential equation model only when there is a vertical predator isocline. It is natural then to ask how this restriction compares with the experimental findings of Huffaker *et al.* (1963). In universes with the greater food supply the peak prey and predator densities averaged 2500 and 98, respectively, per cabinet as compared with the corresponding

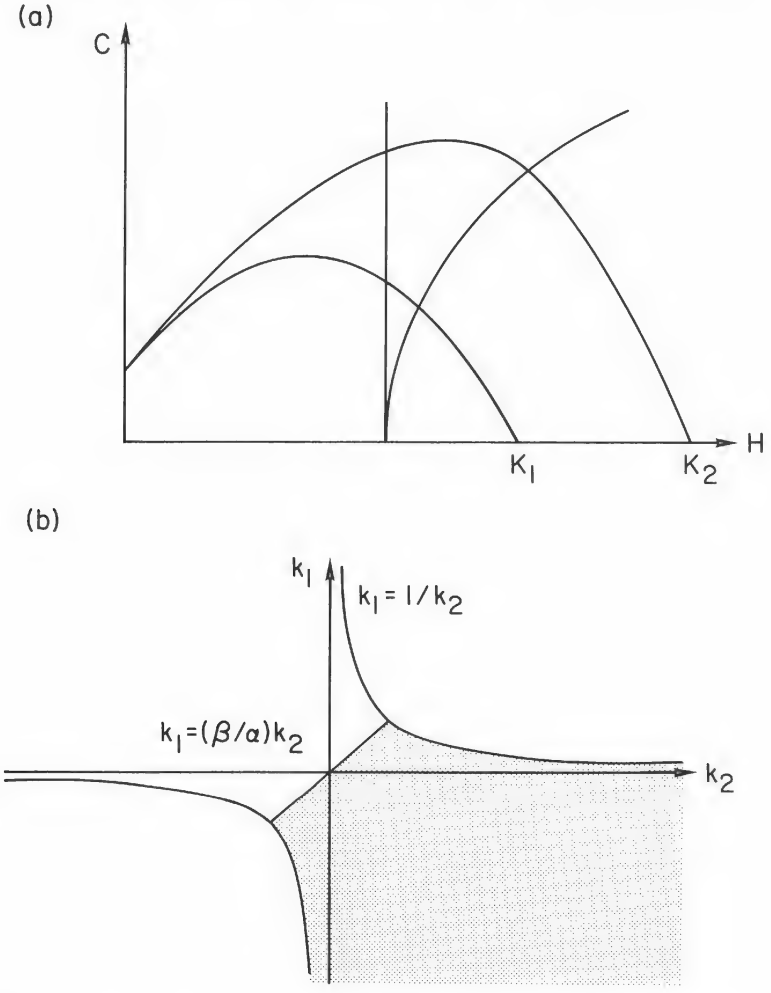

Figure 1. (a) A schematic plot of the prey and predator isoclines relevant to the paradox of enrichment showing the effect of increasing the prey carrying capacity from K_1 to K_2 on the community equilibium point (intersection of isoclines) for no intraspecific carnivore interaction (vertical line or $b_3 = 0$) and for intraspecific carnivore competition ($b^3 > 0$). For the experiments of Huffaker *et al.* (1963), $K_2 = 3K_1$ and the intersection points measured in number of mites per cabinet were (900, 17) and (2500, 98). (b) The stability region (shading) in the $k_2 - k_1$ for the differential equation model with values of the exploitation parameters $\alpha = \beta = 4.5$.

densities of 900 and 17 for the stable universes with one-third the food supply. Since the predator to prey ratio more than doubled upon enrichment, the result was *near annihilation* of the prey through overexploitation. Observe that a vertical predator isocline which preserved the predator to prey ratio of the experimentally enriched system would have required an equilibrium point of 900 prey and 35 predators per cabinet. Hence the population density data for this experiment strongly suggests a nonvertical predator isocline of a *competitive nature* (see Fig. 1a). In order to devise a model that will predict the occurrence of a paradox enrichment in this instance, we now incorporate the effect of age structure, of a simple kind, in the predator population. We assume, for simplicity, that death in the predator comes only as a consequence of reaching a certain age which coincides with the normal ovipositional period. Then considering $C(a,t)$ to be the population density of carnivores of age a at time t, where we have chosen the same scale for age and time, the continuity-type age structure equation

$$\frac{\partial \tilde{C}}{\partial t} + \frac{\partial \tilde{C}}{\partial a} = 0, \quad 0 < a < 1, \tag{14a}$$

holds. A boundary condition describing the birth rate

$$\tilde{C}(0,t) = r_2[g(H,C)C](t) = h(t) \tag{14b}$$

must be included. Finally our death rate assumption implies

$$C(t) = \int_0^1 \tilde{C}(a,t)da. \tag{15}$$

The von Foerster (1959) equation of (14) can be solved by the *method of characteristics* as follows. Beginning with (14), we introduce the characteristic coordinates ξ,η such that

$$t = t(\xi,\eta) \quad \text{and} \quad a = a(\xi,\eta) \tag{16}$$

where

$$\frac{\partial t}{\partial \eta} = \frac{\partial a}{\partial \eta} = 1 \tag{17a}$$

and

$$t(\xi,0) = \xi, \quad a(\xi,0) = 0. \tag{17b}$$

Thus, from (14) and (17), we can deduce that

$$\mathbf{C}(\xi,\eta) = C[a(\xi,\eta),t(\xi,\eta)] \tag{18}$$

satisfies

$$\frac{\partial \mathbf{C}}{\partial \eta} = 0 \tag{19a}$$

and

$$\mathbf{C}(\xi,0) = h(\xi). \tag{19b}$$

Solving (17) and (19), we find that

$$t(\xi,\eta) = \xi + \eta, \; a(\xi,\eta) = \eta, \quad \text{and} \quad \mathbf{C}(\xi,\eta) = h(\xi). \tag{20}$$

Now inverting the transformation of (16) and (18), we obtain

$$\tilde{C}(a,t) = h(t - a). \tag{21}$$

Then substitution of (21) into the relationship of (15) yields

$$C(t) = \int_0^1 h(t - a)da. \tag{22}$$

Finally, employing the change of variables

$$s = t - a \tag{23}$$

in the integral on the right hand side of (22), the following governing equation for $C(t)$ results

$$C(t) = \int_{t-1}^{t} r_2[g(H,C)C](s)ds \tag{24}$$

upon introducing the explicit form of $h(s)$ from (14b).

Our age structure model retains the differential equation (1a) for the prey but replaces (1b) with the integral equation (24). The construction of this model was inspired by earlier models (Wollkind and Logan 1978) of the predator-prey interaction between the McDaniel spider mite *Tetranychus mcdanieli* McGregor, a pest on apple tree foliage, and its control agent, *M. occidentalis*, an ecosystem very much like the one studied by Huffaker *et al.* (1963). It is a generalization of an age structure model that was developed in (Hastings and Wollkind 1982). The community equilibrium point for the system consisting of (1a) and (24) is identical to that defined by (2). A linear perturbation analysis of that critical point for this age structure system can be shown to yield the following secular equation for λ (Smith and Wollkind 1983):

$$\lambda - (1 - \beta k_2)\kappa(\lambda)\lambda + [\alpha k_1(1 - \beta k_2) + \alpha\beta]\kappa(\lambda) - \alpha k_1 = 0 \tag{25a}$$

where

$$\kappa(\lambda) = \begin{cases} (1 - e^{-\lambda})/\lambda & \lambda \neq 0 \\ 1 & \lambda = 0 \end{cases} \tag{25b}$$

while the parameters appearing in (25a) are to be interpreted just as they were earlier. The stability behavior of this quasi-polynomial secular equation has recently been investigated (Smith and Wollkind 1983). We summarize the results of that analysis for the case of $\alpha = \beta = 4.5$, or more generally when $\alpha\beta > 2\pi^2$, corresponding to the conditions for which Figure 1b was drawn. The stability region in that instance ($\alpha\beta > 2\pi^2$) is bounded by the portion of the hyperbola

$$k_2 = \frac{1}{k_1} \quad \text{for} \quad k_1 \leq -2\sqrt{\frac{\beta}{\alpha}} \tag{26a}$$

and a curve given parametrically by

$$k_2 = \frac{1}{\beta}\left[1 - \frac{1}{2}\left(\frac{\theta \sin \theta}{1 - \cos \theta} - \alpha k_1\right)\right], \qquad k_1 = \frac{-\sqrt{2\alpha\beta - \theta^2}}{\alpha} \quad \text{for } 0 < \theta < 2\pi \tag{26b}$$

as depicted in Figure 2.

Upon examination of this figure in comparison with figure 1, we see that the *destabilizing* effect of age structure now makes it possible to extend the paradox of enrichment to the case of $k_2 > 0$. We first observe from Figure 1a that enriching an originally stable ecosystem involving intraspecific carnivore competition will most likely result in a new equilibrium point for which both $k_1 < 0$ and $k_2 > 0$ have been increased. For $\alpha\beta > 2\pi^2$ there can be instability for any k_2 provided $k_1 > -\frac{\sqrt{2\alpha\beta - 4\pi^2}}{\alpha}$, which is the horizontal asymptote in Figure 2. Hence, given the behavior of k_1 and k_2 with enrichment mentioned above, our age structure model admits the possibility of the paradox of enrichment occurring even in the presence of intraspecific carnivore compe-

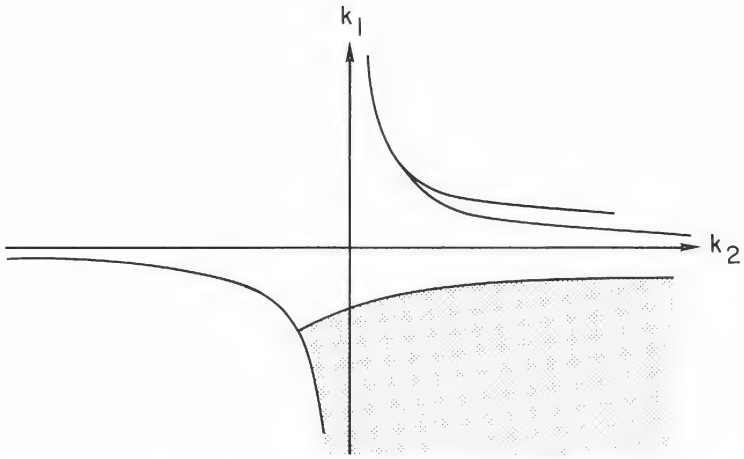

Figure 2. The stability region (shading) in the $k_1 - k_2$ plane for the age structure model with $\alpha = \beta = 4.5$.

tion, and that possibility becomes greater as the parameter $\alpha\beta$, a measure of interspecific interaction, increases. This phenomenon is in accordance with the experimental work of Huffaker *et al.* (1963). Thus the differential equation model without age structure does not predict the occurrence of a paradox of enrichment in this instance, whereas such a prediction is consistent with the stability results of our age structure model.

Validation procedures of this sort are the last step in any example of comprehensive applied mathematics. The latter involves taking some real world phenomenon, modeling it mathematically, and thereby making theoretical predictions which are then tested against observables of the phenomenon. The higher this correlation is, the better the model is judged to be. In other words, the proof of such an applied mathematics pudding is in the eating.

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Age Distribution of Western Hemlock and Its Relation to Roosevelt Elk Populations in the South Fork Hoh River Valley, Washington

Abstract

The relationship between historical fluctuations of Roosevelt elk populations and the age structure of western hemlock was examined in two terrace forests in the South Fork of the Hoh River. Despite a dramatic decrease of elk between 1895-1910, no evidence was found for an increase in hemlock establishment during this period. Since 1700, hemlock establishment has remained low (1-6 trees per 2 ha per decade) on the lower terrace but increased in the upper terrace forests between 1830-1900. Neither age-class structure is consistent with the hypothesis that elk browsing on hemlock is so severe that trees become established when elk populations are low.

Introduction

Valley bottoms on the western slopes of the Olympic Mountains are noted for their tall, epiphyte-laden forests of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*). These alluvial stands contrast with many others in the coastal *Picea sitchensis* zone in their relative openness and successful reproduction of Sitka spruce (Franklin and Dyrness 1973, McKee *et al.* 1980).

The Roosevelt elk (*Cervus elaphus roosevelti*) is an important part of the valley ecosystems. Some reside permanently in the valleys, whereas many Roosevelt elk use these areas as winter range only (Jenkins and Starkey, 1980). Browsing by elk is known to have major effects on the structure and composition of plant communities (Sharpe 1956), and intense browsing has been noted by many authors (Bailey 1918; Murie 1934, 1935; Schwartz and Mitchell 1945; Sumner 1938).

Western hemlock reproduction is currently not as well represented as Sitka spruce in many of the alluvial forests, and differential browsing by Roosevelt elk has been proposed as an explanation. Western hemlock is a component of the elk's winter diet, but Sitka spruce is rarely browsed (Leslie and Starkey 1980).

A test of the elk-browsing hypothesis was suggested in 1978, when a disproportionate number of pole-sized (10-30 cm) western hemlocks were found during structural analysis of some alluvial forests (McKee *et al.* 1980). Since Roosevelt elk populations were known to have been low around 1900 (Jenkins and Starkey 1980; Taber and Raedeke 1980), this bulge in the western hemlock size-class distribution might be related to relative freedom from browsing. Assuming that elk ate western hemlock in the past, fewer elk could mean that more hemlocks escape destruction as saplings and grow into trees.

The study reported herein was designed to test this hypothesis by developing an age-

class distribution of western hemlocks and relating it to elk populations. The study was carried out in two river terrace forests of Sitka spruce and hemlock along the South Fork of the Hoh River in Olympic National Park. The results are, therefore, applicable only to that valley.

Study Area

The study sites are permanent sample plots established in 1978 within the valley of South Fork of the Hoh River on the western slope of Olympic National Park (Franklin 1980). The South Fork is a typical U-shaped valley of glacial origin, but has an unusually wide floodplain. The plots are located on the upper three of six terrace surfaces; the upper terrace plots characterized the forests found on surfaces five and six, but the lower terrace plots characterize forests on surface four (Swanson and Lienkaemper 1980). Soils on the lower terrace plots are haplaquepts, whereas those on the upper terrace plots are dystrochrepts (Joseph Means, pers. comm.). The climate is moist and mild, with mean annual precipitation near 320 cm and a mean annual temperature of 10°C (Franklin 1980).

Coniferous forests of Sitka spruce and western hemlock found on the river terraces have many notable features, including: (1) heavy cover of epiphytic plants (Franklin and Dyrness 1973); (2) a canopy layer that can exceed 85 m in height (McKee *et al.* 1980); and (3) despite the tall structure, an open canopy which allows a dense herb layer or tall shrub layer (or both) to develop. Upper and lower terrace plots had 142 and 64 trees ha^{-1}, respectively, and the estimated biomass for the same stands was 808 and 642 mt ha^{-1} (McKee *et al.* 1980). "Nurse-logs" are the most important site of tree reproduction, with 88 to 97 percent of all seedlings starting on logs (McKee *et al.* 1980). Logs cover only a small fraction of the total surface; however, Graham (1980) found log coverage of 11 percent on the upper terrace and 6 percent on the lower terrace.

Roosevelt elk are common, although no historical or current population estimates are available for the South Fork valley. Historical data suggests that elk were plentiful over the Olympic Peninsula until 1895. Rapid settlement during the 1890s led to a dramatic increase in hunting and a subsequent drop in elk numbers. By 1905, populations were so low that the state legislature declared a 10-year moratorium on elk hunting. In 1909, the Federal government set aside a reserve for the elk. The recovery of the elk was sufficiently rapid that heavy browsing of the vegetation was reported by 1915. A large elk die-off during the winter of 1916-17 may have been a consequence of this overbrowsing. Other sequences of population increase, overbrowsing, and population decrease evidently have occurred around 1933, 1937, 1949, 1956, and 1964, and may represent an important feature of elk population dynamics in the Olympic National Park (Jenkins and Starkey 1980).

Methods

Two 2-ha permanent sample plots were established in 1978 (Franklin 1980), one each on the upper and lower terraces. Trees over 5 cm diameter at breast height (dbh) were mapped, tagged, and measured for dbh on the plots at that time. Most of the western hemlocks were cored during the summer of 1981. Since we were interested primarily in trees less than 200 years old, few individuals over 90 cm dbh were cored (see Fig. 1). The cores were taken at breast height, numbered according to the tree tags, and stored

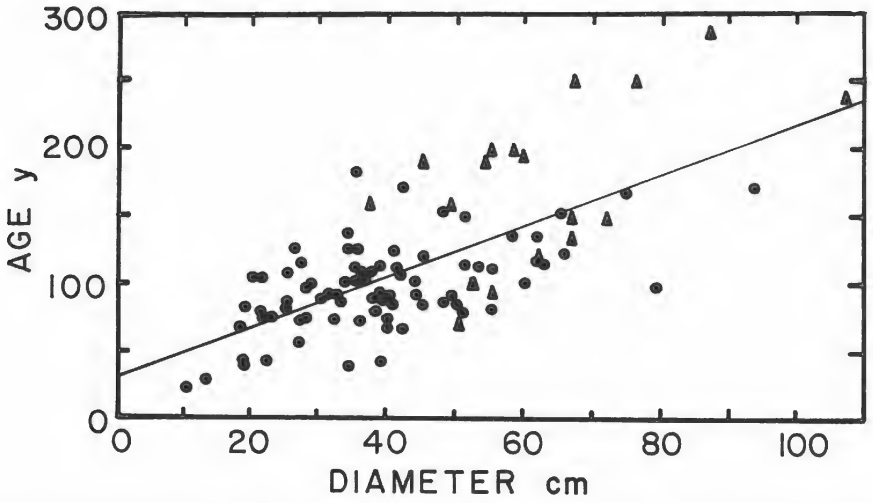

Figure 1. Relationship between diameter at breast height (dbh) to age at breast height (abh) for *Tsuga heterophylla* in upper terrace forest. Dots represent ages for trees without heartrot, while the triangles indicate trees with heartrot and estimated ages. The line drawn through the points was fitted by linear least-squares and is ABH = 30.5 + 1.8 DBH, $r^2 = 0.46$, N = 95. DBH is in cm and ABH is in years.

in plastic straws for 2 to 4 weeks until rings could be counted. Cores with very slow growth rates were aged with the aid of a hand lens. Heartrot made 35 percent of the cores incomplete. Ages of these trees were estimated by assuming that the innermost decade of growth represented the growth rate of the missing part of the radius and that the first ring lies in the center of the bole cross section. To estimate the total age of an individual, years required to reach breast height were assumed to be 10. Trees were grouped into decade age groups for analysis. The age structure of small hemlock (5 cm dbh) was estimated in each plot by separating individuals into 5-year age classes based on bud scars and branch whorls. A regression of age against branch whorls for hemlock indicated a close relationship between the two variables (age = 1.44 + 0.94 whorl numbers, $r^2 = 0.79$, N = 26, $p < 0.01$). Plants with repeated browse damage were assumed to be older than bud scars would indicate. In each terrace plot, hemlocks were examined in eight, 50 m by 1 m belt transects. Relative estimates of elk population size for the Olympic Peninsula are based on Taber and Raedeke (1980). Precipitation and temperature data between 1914 and 1980 for the Forks, Washington, weather station were compiled from U.S. Weather Bureau summaries (1914-1980).

Results and Discussion

The age structure of western hemlock on terraces does not appear to correspond well with estimated elk population sizes (Fig. 2). More hemlocks do not appear to have become established when elk densities were lowest. On the lower terrace forest peaks of western hemlock establishment occurred during the decades of 1880, 1840, and 1800; but until 1900, the overall pattern was of two to six trees per 2 ha established per decade. On the upper terrace there was a period of heavy establishment (8 to 21 trees per ha per decade)

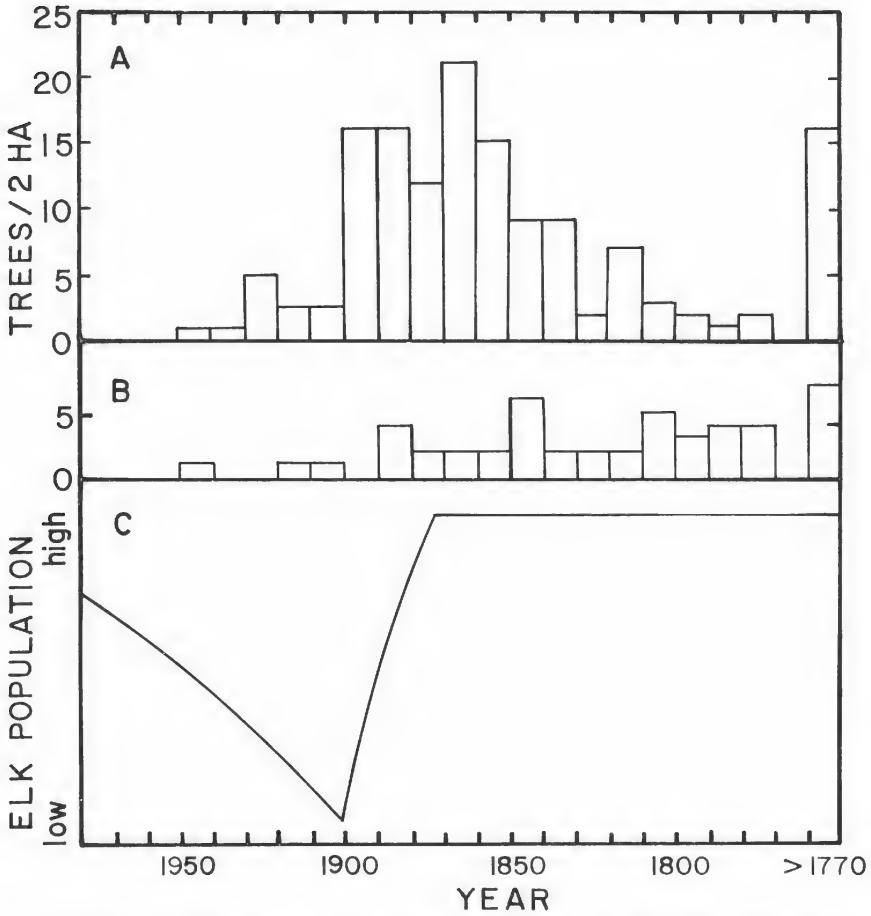

Figure 2. Density of *Tsuga heterophylla* by decade age classes for upper and lower terrace stands as a function of elk population fluctuations recorded for the Olympic Peninsula. A. upper terrace B. Lower terrace C. Relative fluctuations in elk populations.

between 1830 and 1900. This period does not correspond well to the hypothesized elk decline between 1890 and 1910. One peak in hemlock establishment on the upper terrace could be related to a decline in elk during the 1930's, but the absence of such a pulse on the lower terrace indicates factors other than elk are controlling hemlock establishment.

Hemlocks less than 20 years old show a reverse-j shaped population-age structure (Table 1.) Survival rates of 54 to 64 percent per yr were calculated by assuming that a constant percentage survive each year during the 5-year age classes.[1] These low survival rates may be caused by a number of factors, including seasonal water stress and low nutrient availability on logs (especially less decayed ones), competition, and elk browsing. Elk kill plants by repeated browsing of tops as well as by pulling root systems out of

TABLE 1. Age structure of **Tsuga heterophylla** less than 5 cm dbh for upper and lower terrace levels. Each number is based on eight, 50 m by 1 m belt transects.

Age class (years)	Density* (number/50 m^2)	
	Upper terrace	Lower terrace
0-5	51.37 ± 49.64	50.00 ± 47.98
5-10	2.37 ± 0.71	1.50 ± 2.14
10-15	0.25 ± 0.16	0
Total	53.99 ± 50.60	51.50 ± 48.87

*Mean ± standard deviation.

logs. Studies using small exclosures (Dee Boresma, pers. comm.) have confirmed that elk reduce hemlock survivorship.

Alternative explanations of the western hemlock age distribution other than elk include small mammals, fire disturbance, windstorm, or climatic changes. Other mammals, such as mountain beaver (*Alpodontia rufa*) or snowshoe hare (*Lepus americanus*), may also influence hemlock reproduction and therefore reduce the correlation between elk populations and hemlock age structure. Although there was no evidence of fire in these plots (McKee *et al.* 1980), other terrace forests in the area have burned. Graham (1980) failed to find evidence for a large blowdown on either terrace, so this disturbance seems to be an unlikely explanation.

Climatic changes also are an unlikely explanation. First, if climatic changes were important, they were interacting with some other factors, since there is little correspondence between hemlock peaks in establishment in the upper and lower terraces. Second, climate changes, as reconstructed from tree rings for the Columbia River Basin (Fritts *et al.* 1979), do not match changes in hemlock age classes. For example, Fritts *et al.* (1979) found precipitation 20 mm over the 1901-70 mean for the 1850's, and precipitation 20 mm below the mean for the 1860's. Yet both decades were similar in hemlock establishment on the upper terrace. Finally, there has been no consistent long-term change in climate in terms of precipitation or temperature that corresponds to the decrease in Tsuga establishment since 1930 (Fig. 3).

At present we hypothesize that the pulses in *Tsuga* for the two terraces are associated with some phases of stand development, such as canopy openings or seedbed, which could be secondarily influenced by elk and climate. Establishment of western hemlock would be sensitive to the abundance of rotten wood (McKee *et al.* 1980) and changes in light regime. During the period of 1830 to 1900, one or both of these conditions may have been more favorable in the denser upper terrace stand. Fluctuations on the lower terrace were probably minor. A detailed analysis of stand history, such as that done by Henry and Swan (1974), would be very revealing in this regard. Finally, we want to emphasize that there may be a poor correspondence between hemlock establishment and historical elk population fluctuations in other watersheds. The results of this study suggest that age and not size structure should be examined before any relationships are assumed between elk and tree establishment.

Acknowledgments

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[1]The exact calculation is as follows: percent survival $= \left\{ \frac{\text{number at t+1}}{\text{number at t}} \right\} 0.20$

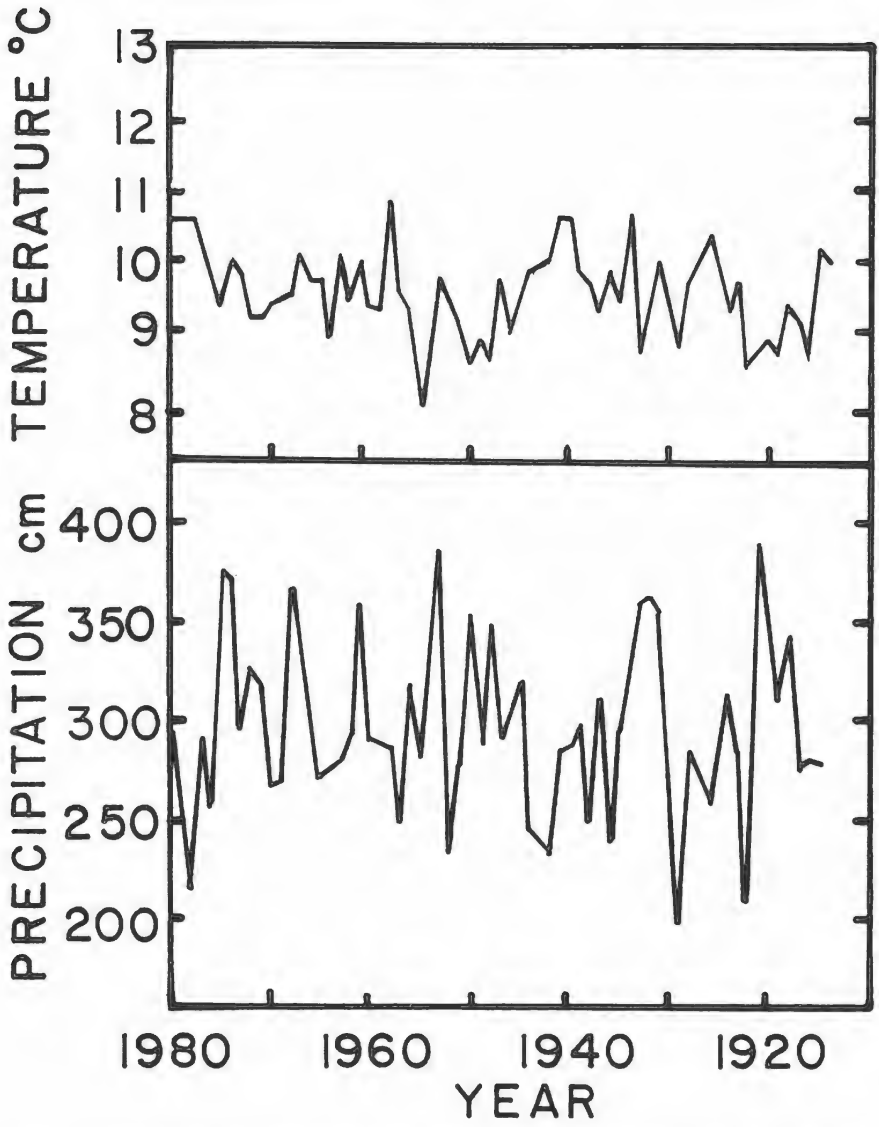

Figure 3. Mean annual temperature and total annual precipitation between 1914 and 1980 for Forks, Washington.

McKee and Dr. Glenn Hawk shared data from their 1978 stand inventory. Thanks are also extended to Ranger Howard Yanish, who provided logistical support during field work.

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The Influence of Geology on the Chemical Composition of Two Washington Rivers

Abstract

The Hoh and Nisqually rivers of western Washington originate in major national parks having similar vegetation but dissimilar geology. The Hoh River, originating from three glaciers on the flanks of 2428 m Mt. Olympus, drains approximately 80,000 ha underlain by marine sediments, primarily a $CaCO_3$ cemented graywacke. The Nisqually River, originating from glacier melt on 4392 m Mt. Rainier, drains approximately 150,000 ha underlain by flows of pyroxene andesite. Differing bedrock mineralogy results in striking differences in major ion concentrations between rivers. Ionic concentrations increase rapidly within undisturbed national parks but remain relatively stable, maintaining characteristic differences, as rivers traverse lower watersheds influenced by forestry, farming, and urbanization. With minor exceptions, geochemical reactions control the chemical composition of the Hoh and Nisqually rivers.

Introduction

Major factors influencing the chemical composition of streams and rivers include mineralogy, vegetation, climate, and man. The relative importance of each control, however, is often masked by group interactions, making interpretation of individual contributions to stream composition difficult.

One method of assessing the relative importance of an individual process is to hold all others constant, a formidable task in the real world. An alternative is to choose study areas similar in all but one major attribute. In this paper, insights into geochemical processes controlling river composition are provided by contrasting two watersheds similar in all significant physical characteristics except bedrock mineralogy.

The Hoh and Nisqually Rivers are major drainages of western Washington, draining sedimentary and igneous rocks, respectively. Both rivers are glacier fed and originate at relatively high elevations within national parks. Their initial composition is not influenced by developed soils, vegetation, or man, and these factors do not affect either river until merging of the first major tributary, about 7 km downstream for the Hoh, and 5 km for the Nisqually. Above these points, water composition is controlled by melt-water composition (snow-ice) and rapid geochemical reactions between water and local rock.

I believe that contrasting mineralogy is the key to explaining compositional differences between these watersheds. And I propose that the low temperature origin of the Hoh River sedimentary rocks make them less susceptible to chemical attack than the igneous, andesitic rocks of the Nisqually River, and that these differences in mineral stability are reflected in their respective drainage water composition.

Study Area

The Hoh River, beginning at the terminus of the Hoh Glacier on the northern flanks of 2428 m Mt. Olympus, drains the western interior of Washington's Olympic Mountains

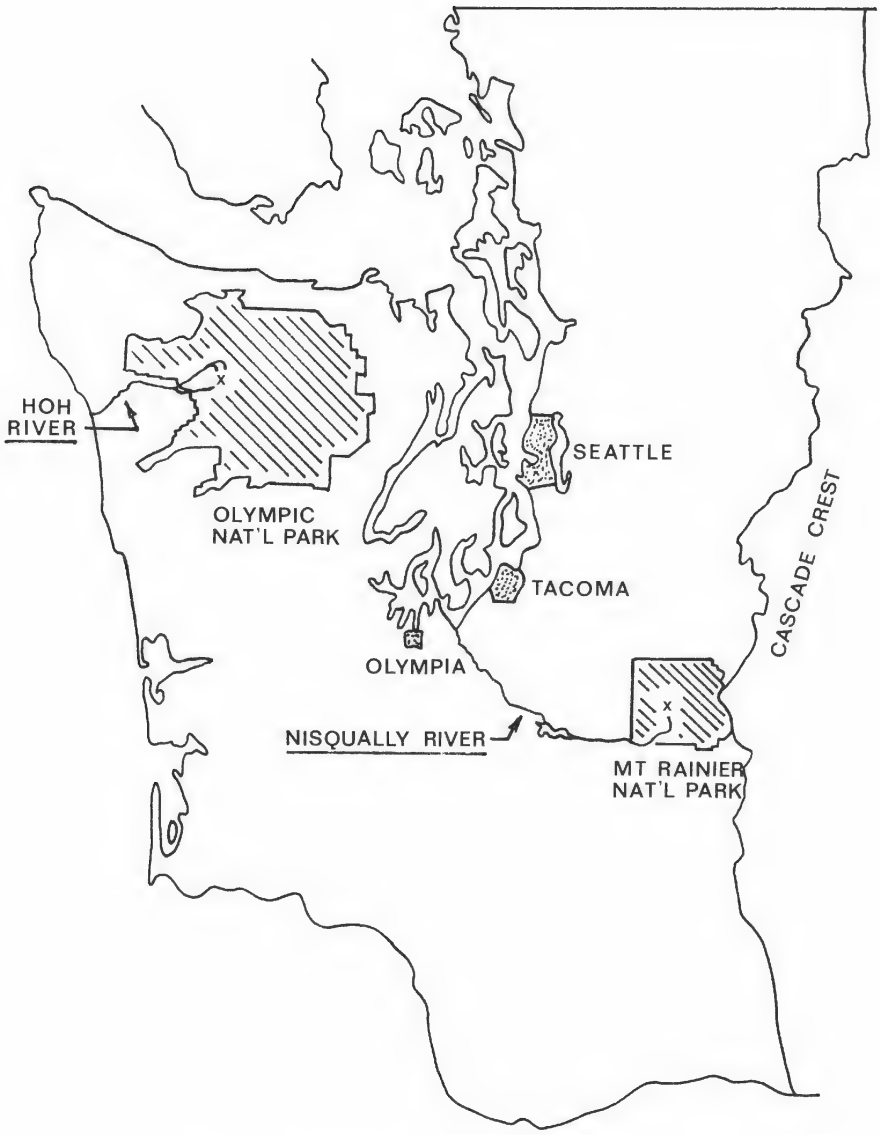

Figure 1. The Hoh and Nisqually rivers, major drainages of western Washington, originate from glaciers within the Olympic and Mt. Rainier National Parks, respectively.

(Fig. 1). Similarly, the Nisqually River emerges from an ice cave at the terminus of Nisqually Glacier, a 7 km long valley glacier on the southern flanks of 4392 m Mt. Rainier. The Nisqually River has the larger watershed, approximately 100 km long and draining about 1900 sq. km between the Cascade Mountains and Puget Sound. The Hoh water-

shed, approximately 90 km long, drains about 800 sq. km and terminates at the Pacific Ocean. Both rivers are relatively undisturbed by man's activities for a portion of their lengths, with the first 40 km of the Hoh River within the Olympic National Park (ONP) and the first 20 km of the Nisqually River within Mt. Rainier National Park (RNP). About 20 km after leaving Mt. Rainier National Park, the Nisqually River enters Alder Lake (LAKE), the first of two power generation impoundments. The Hoh River is unrestricted by man made structures for its entire length.

Climate and Hydrology

The Hoh River watershed, because of its proximity to the ocean, receives the most annual precipitation, 230 cm along the coast and increasing to an estimated 600 cm on Mt. Olympus. Precipitation over the Nisqually watershed ranges from 100 cm along Puget Sound to about 350 cm over Mt. Rainier. Although its watershed covers only one half the area, heavy precipitation results in greater mean annual flow for the Hoh (57 m^3/sec) than for the Nisqually River (44 m^3/sec). Annual runoff of the Hoh River is approximately 335 cm, while that of the Nisqually is 104 cm. These differences, however, are not considered important to this study, as size and runoff of a watershed have little influence on final concentrations of dissolved constituents (Hembree and Rainwater 1961). Also, climatic differences are primarily restricted to winter, whereas data presented here were collected during the summer when flow was controlled by glacier melt.

Vegetation

Except for the lack of a *Picea sitchensis* (Bong. [Carr.]) zone in the western Cascades and the unique "rain forests" of lower Olympic valleys, forest types of the two regions are similar. Starting in the *Tsuga heterophylla* (Raf. [Sarg.]) zone of the Puget Sound lowlands, vegetation of the Nisqually watershed passes through montane *Abies amabilis* (Dougl. [Forbes])—*T. heterophylla* and subalpine *A. amabilis—Tsuga mertensiana* (Bong. [Carr.]) forests to the open alpine meadows of Mt. Rainier (Fonda and Bliss 1969). A similar sequence occurs in the western Olympics, where dense coniferous forests cover the slopes from sea level to 1800 m. The *P. sitchensis* zone, occurring from sea level to 150 m in the western Olympics, is followed by a limited *T. heterophylla* zone with the *A. amabilis—T. heterophylla* community as the most extensive, occurring from 550 to 1100 m on all ridges stretching from Mt. Olympus to near the ocean. Dominant species in subalpine forests are again *A. amabilis* and *T. mertensiana.* Alpine vegetation of either watershed is not extensive, with ground above timberline occupied primarily by glaciers, snowfields, or bare rock.

Geology and Mineralogy

Marine sediments of the Soleduck Formation underlie the Hoh River watershed and comprise the core of the Olympic Mountains (Danner 1955). Uplifting of the Olympics occurred simultaneously with the uplifting of the Cascades, with subsequent erosion producing the major peaks, including Mt. Olympus. The slightly metamorphosed sedimentary rocks include shale, siltstone, sandstone, and graywacke.

Sandstone is light gray to brown, composed of quartz, feldspar, and muscovite grains, while graywackes are dark gray to black and are composed of dark colored rock fragments mica, feldspar, and quartz grains. Plagioclase feldspars are probably albitic, as Na-rich feldspars generally predominate in sedimentary sandstone (Pettijohn 1963). Potash and

soda feldspars offer greater resistance to chemical attack, persisting as detrital grains in sedimentary rock (Loughnan 1969). The mica is primarily muscovite, one of the most resistant of the silicate minerals to weathering. Rapidly weathering biotite is not believed an important mineral constituent of these sedimentary rocks. Calcite is a cementing agent in sandstone and graywacke and is also abundant, along with quartz, in the many cracks and fissures formed as the strata were uplifted. The sulfur bearing minerals, gypsum and pyrite, are also common, and phosphorus is present in the mineral apatite (Larson 1979). Shell debris, however, may be an equal or greater phosphate source (Pettijohn 1963).

Mt. Rainier, source of the Nisqually River, is a quaternary volcano composed primarily of flows of pyroxene andesite (Fiske *et al.* 1963). The mountain is built on an earlier surface of altered volcanic and sedimentary rock. Volcanics, correlated with basalts of the Willapa Hills to the west or the andesitic and basaltic flows in the Cascades to the east, also underlie the lower Nisqually watershed (McKee 1972).

In contrast to the mineralogic variability of marine sediments, lava flows from Mt Rainier were remarkably similar in composition throughout the mountain's history (Fiske *et al.* 1963). Mineralogy of andesites is uniform with andesine, the major plagioclase feldspar, and orthoclase, the primary K-feldspar. The dominant dark colored mineral is the pyroxene, hypersthene. Slightly subordinate in abundance to hypersthene is augite, with olivine, a third ferromagnesiam mineral, present in minor quantities. Many additional minor accessory minerals are present, but only two are of interest here, the phosphate mineral apatite, associated with the volcanic rocks, and pyrite, found in hydrothermal deposits.

Methods

The compositional evolution of the Hoh and Nisqually Rivers was developed by measuring dissolved ion concentrations at selected points along each river, starting at the glacier and proceeding to the mouth. Sampling of the Hoh River began at the Blue Glacier rather than the relatively inaccessible Hoh Glacier, with the final Hoh River sampling location about 300 m inland from the ocean. The final Nisqually River sampling location was just upstream of the Nisqually delta.

Composition of the Hoh River was determined at 16 locations, nine inside the Olympic National Park and seven outside. The lower nine locations, accessible by road, were sampled three times during June and August 1979, whereas the upper seven locations (first 25 km), accessible only by trail, were sampled once in August. Because of the overhanging terminus of the Blue Glacier and the inaccessibility of the canyon through which Glacier Creek flows, the first sampling of the Hoh River was about 7 km downstream from Blue Glacier near the confluence of Glacier Creek and the Hoh River. Sampling above this point included ice melt near the glacier terminus (0 km downstream) and a small tributary of Glacier Creek fed by a combination of ice and snow melt (about 1 km downstream).

Composition of the Nisqually River was determined at 13 locations, seven inside Mt. Rainier National Park and six outside, including one location midway along Alder Lake. Locations were sampled twice, in September and early October 1979, with additional preliminary sampling of the two lowest stations in June. Again, in addition to the downstream sequence, both glacier melt water and the Nisqually River as it emerged from the glacier ice cave were sampled. I assumed the Nisqually River originates at the glacier terminus, ignoring subglacial flow.

Water temperature and pH were measured in the field and duplicate 250 ml water samples collected at each location for laboratory analysis of selected dissolved ions. Samples were refrigerated until analyzed. Analyses requiring special instrumentation followed procedures provided by the equipment manufacturers. Concentrations of respective ions were averaged for each sampling location to obtain a mean value.

A meter equipped with automatic titrator measured alkalinity and pH; alkalinity, primarily bicarbonate (HCO_3), was determined by acid titration to a pH 4.5 end point. A YSI model 31 conductivity bridge measured specific conductance in micromhos/cm. An Instrumentation Laboratory Atomic Absorbtion Emission Spectrophotometer measured the dissolved cations calcium (Ca), magnesium (Mg), sodium (Na), potassium (K), and iron (Fe).

A Technicon II Autoanalyzer measured nitrogen as nitrate (NO_3–N) and ammonium (NH_4–N), phosphorus as orthophosphate (PO_4–P), sulfur as sulfate (SO_4), and chloride (Cl). Nitrate was determined by reducing it to nitrite using a copper-cadmium reductor column. The Berthelot reaction was used to determine NH_4–N, the molybdenum blue method, PO_4–P, and the methylthymol blue method, SO_4. Chloride was mixed with mercuric thiocyanate, liberating thiocyanate ion, which in the presence of ferric ion formed a highly colored ferric thiocyanate proportional to the original Cl concentration.

An ammonium molybdate-heteropoly blue procedure was used to determine silica (SiO_2) using instructions and premixed chemicals obtained from Hach Chemical. Color intensity was measured at 650 nm on a Bausch and Lomb Spectronic 70 spectrophotometer.

Results and Discussion

Compositional trends for each river were developed by plotting the average concentration of selected ions at individual sampling locations against distance downstream from the glacier (Fig. 2-5). Vertical bars represent the standard error of the mean, but no bar indicates that either a single sample (Hoh 0-25 km) or the standard error was less than the symbol size. Although sample size is small, significant differences between the two rivers were apparent for most ions.

The hydrogen ion concentration in both rivers decreased rapidly over the first few km, simultaneous with increases in conductance (Fig. 2). The pH of melt water increased from near 6.0 for the Hoh and 6.5 for the Nisqually, to over 7.0 during the first km of travel. Similarly, the specific conductance of both rivers increased from about 5 to over 30 micromhos/cm.

The rapid increase in ion concentrations occurred until the solution potential was depleted. Subsequent to this increase, rock dissolution was apparently slow, with little additional change in stream composition. The hydrogen ion decline slowed within 10-15 km, with little downstream change in pH for either river over the remaining 60-80 km of river length. The rise in conductance of both rivers also slowed abruptly after 20 to 25 km.

Although pH and conductance behaved similarly down both rivers, actual values differed, with pH and conductance of the Nisqually River generally lower than corresponding values for the Hoh. Considering specific conductance (Fig. 2) as a general measure of ion concentrations, the higher conductance of the Hoh River was contrary to

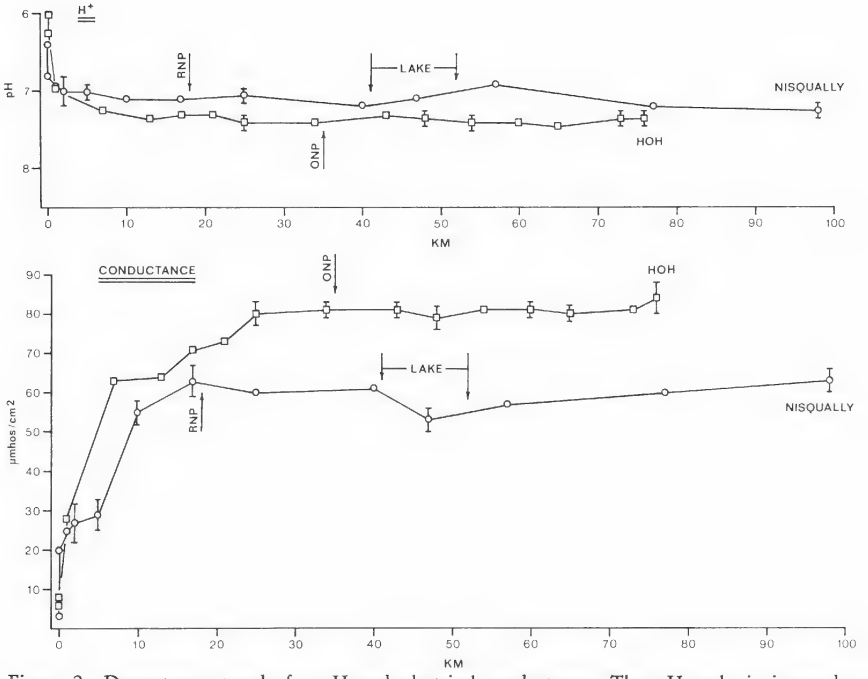

Figure 2. Downstream trends for pH and electrical conductance. The pH scale is inverted to portray the decrease in hydrogen ion concentration.

expectations. The marine sediments of the Hoh basin, having already survived one weathering cycle, were expected to exhibit greater resistance to chemical denudation than the volcanics of the Nisqually basin. This anomaly, however, is explained by the downstream trends in cation concentrations (Fig. 3), with the high Hoh River conductance an artifact of calcite weathering.

The Ca concentration of both rivers increased downstream, mirroring their respective conductivity trends, with a rapidly increasing initial concentration and leveling off after 15-20 km of stream travel (Fig. 3). Concentrations of Ca in the Hoh River greatly exceeded those of the Nisqually, reflecting the abundance of readily dissolved calcium carbonate in the Hoh watershed. The Ca concentration of the Nisqually River increased slower than that of the Hoh, with a lower final concentration, probably related to weathering of andesine and Ca-rich augite, silicate minerals being inherently more stable than calcite in these slightly acidic dilute solutions. That the higher conductance of the Hoh River is related to its Ca content (and associated anions) is indicated by the trend reversals found for remaining cations (Fig 3). In contrast to Ca, other cations had highest concentrations in the Nisqually rather than the Hoh River.

In general, downstream increases in the Mg concentration of both rivers were less rapid than Ca increases. But like Ca, differences in Mg concentrations between rivers were well defined (Fig. 3). The higher Mg concentration in the Nisqually River is probably related to the presence of pyroxenes, while the source of Mg in the Hoh River is probably vermiculite or chlorite (Larson 1979), silicate minerals having greater

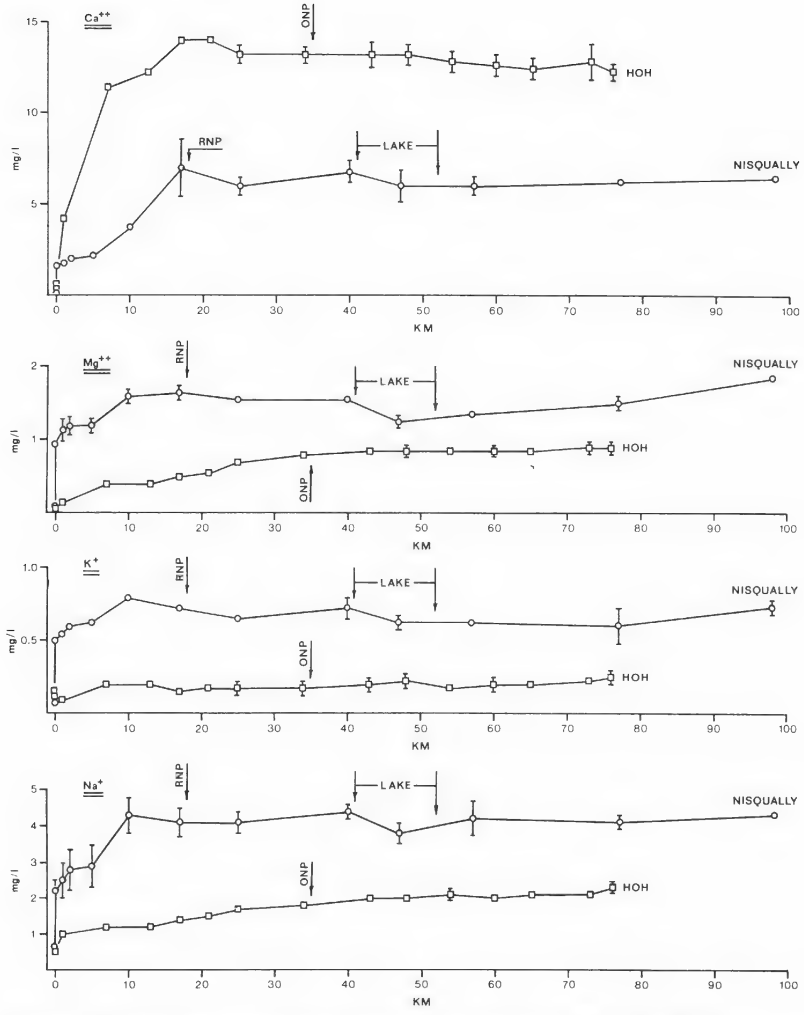

Figure 3. Downstream concentration trends for the cations Ca, Mg, K, and Na.

weathering resistance than pyroxene. A possible carbonate source for some of the Mg in the Hoh River is the mineral dolomite. However, a final 5:1 Ca/Mg mole ratio for Hoh River water, rather than the 1:1 expected for waters draining dolomite, indicates that unless there is a geochemical sink for Mg, the source of the carbonate is primarily calcite and not dolomite.

Downstream trends for K and Na were similar to those of Mg, with highest concentrations in the Nisqually River (Fig. 3). The major source of K in the Nisqually is probably orthoclase feldspar, whereas the low K concentration of the Hoh is controlled by its concentration in ice melt (precipitation) and not by any watershed contribution. Subtracting the K in Blue Glacier melt water from the final Hoh River concentration

leaves only a small residual originating within the basin. A similar calculation for the Nisqually indicates a much greater watershed contribution. The small K increase in the Hoh River is probably due to weathering of the mica, muscovite. The greater increase in K concentration within the Nisqually basin reflects the lesser resistance to chemical weathering of orthcoclase as compared to muscovite.

The Na concentration of the Hoh River, like K, is controlled by its concentration in ice melt, with only a gradual downstream increase from weathering of Na-rich feldspars. The source of Na in the Nisqually River is probably andesine, with the higher concentration suggesting that the andesine is less resistant to weathering than feldspars of the Hoh River marine sediments. That the source of Na in the Nisqually, as well as much of the Ca, is a feldspar is indicated by a Na:Ca mole ratio of 1.2, similar to the 1.5 ratio of average Mt. Rainier andesine. The ratio in Hoh River water is about 0.3 and is completely dominated by the Ca from carbonates.

The development of SiO_2 concentrations as waters move downstream supports preceding interpretations of cation differences. Silca is not an important component of forest vegetation; yet a rapid initial increase in silica, similar to the cations, occurred in both rivers (Fig. 4). The increasing silica concentrations reinforce the concept of chemical weathering as the major control of river composition, with differences in ion concentrations between rivers related to mineralogy. Silica concentrations were higher in the Nisqually than in the Hoh River, indicating greater silicate weathering in the Nisqually watershed.

As with preceding ions, concentrations of the anions HCO_3 and SO_4 increased rapidly during the first few km of river travel (Fig. 5). Both anions had higher concentrations in the Hoh than in the Nisqually River and followed trends similar to Ca. Hydrolysis of readily dissolved carbonate minerals is the major source of high bicarbonate concentrations in the Hoh River, while the major source of HCO_3 in the Nisqually River is acid weathering of silicates. The greater resistance to chemical weathering of silicates, as compared to carbonates, is reflected in the lower HCO_3 concentration of the Nisqually.

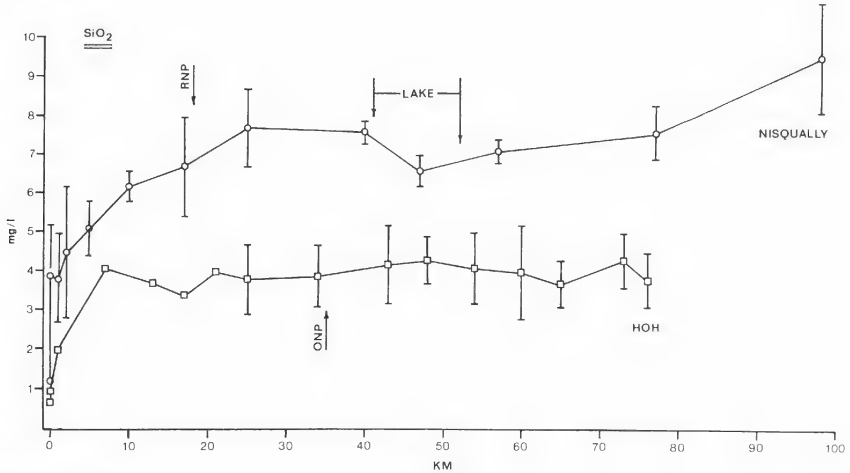

Figure 4. Downstream concentration trends for SiO_2.

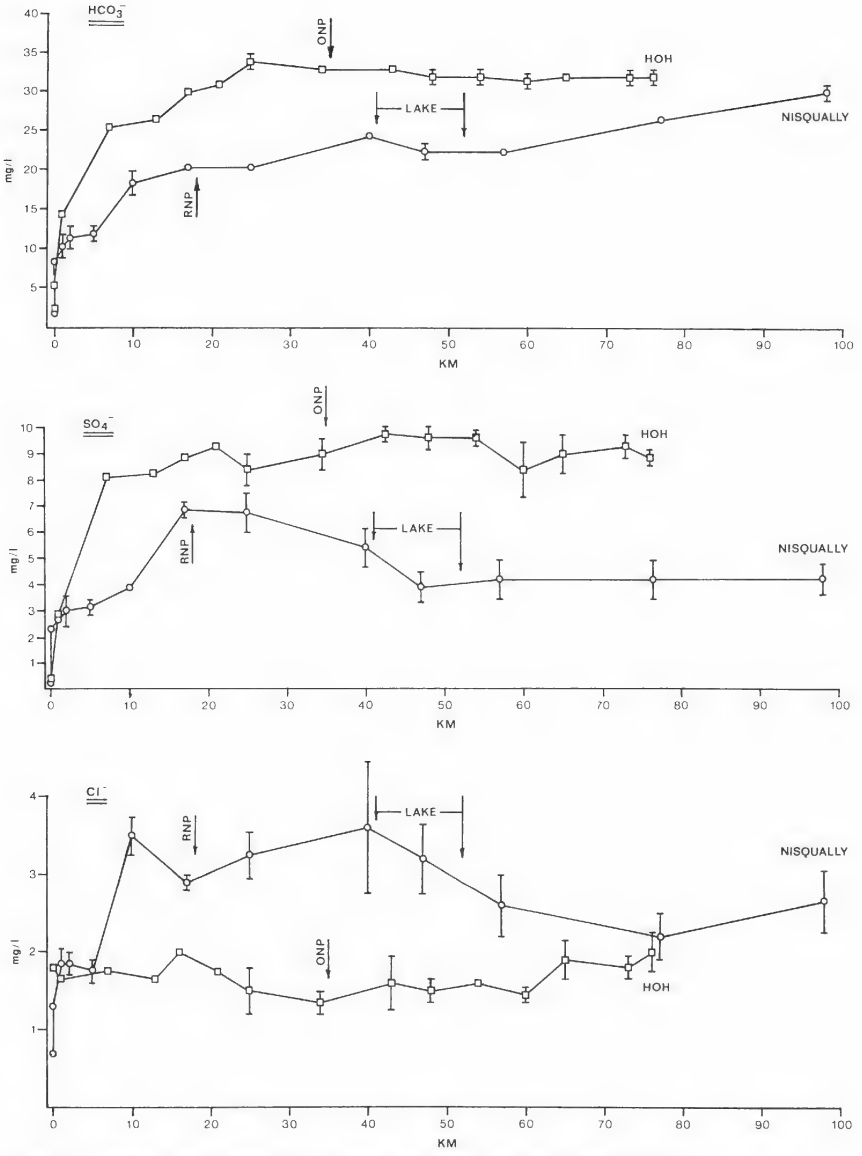

Figure 5. Downstream concentration trends for the anions HCO_3, SO_4, and Cl.

The rapid increase in Hoh River SO_4 concentration and the slow rate of pyrite oxidation suggest that, although pyrite is the usual S-bearing mineral in sediments (Hem 1970), sulfur is present in the Hoh watershed as the secondary sulfate mineral, gypsum. Sulfuric acid, a product of pyrite oxidation, will react with calcite to produce gypsum (Keller 1962), and sulfates are often found as a component of sandstone cements (Petti-

john 1963). Both minerals are probably present, pyrite having formed under initial reducing conditions with subsequent partial conversion to gypsum.

In contrast to the Hoh, lower SO_4 concentrations in the Nisqually River are probably related to the primary mineral, pyrite. Pyrite oxidation is usually accompanied by a pH decrease, while gypsum dissolution is not, an observation compatible with the lower pH of the Nisqually River. Additionally, the Nisqually River had generally higher Fe concentrations than the Hoh River, an average of 0.47 mg/1 versus 0.06 mg/1, which supports a FeS_2 source for SO_4.

The anion Cl differed from HCO_3 and SO_4, with highest concentrations in the Nisqually rather than in the Hoh River (Fig. 5). Hoh River concentrations were nearly constant, controlled by a relatively high Cl concentration in melt water. The high melt water concentration is probably related to the Blue Glaciers proximity to the ocean. High Cl concentrations in the Nisqually are more difficult to interpret, as Cl is generally considered a minor constituent of volcanic rock. The low Cl concentration of Nisqually ice melt has little influence on the final Nisqually River concentration, and major Cl increases occur within Mt. Rainier National Park, where salt use by man is negligible. Other inevstigators (Hem 1970) found similar Cl anomalies in their studies; the only feasible Cl source being the underlying crystalline rock supposedly devoid of Cl. Three possible sources of significant Cl are fluid inclusions formed during cooling of the original magma, ferric chloride, a sublimate found near volcano vents, and HCl, a common magmatic gas.

Concentrations of the N and P ions had the greatest spatial and temporal variation, and their trends were the most difficult to interpret. Concentrations of NH_4 were similar in both rivers (0.01 to 0.08 mg/1), and aside from high variability, final concentrations did not differ greatly from those of glacier melt. Nitrate concentrations were also similar for waters draining the upper watersheds (0.002 to 0.040 mg/1). Increased concentrations (0.090 to 0.095 mg/1) were found at the two lowest Nisqually sampling stations and were possibly a result of extensive livestock grazing in the lower Nisqually valley. Phosphate concentrations in the Nisqually River were initially greater than those of the Hoh (0.005 vs. 0.020 mg/1) but dropped to a concentration similar to the Hoh within 25 km. Similar concentrations and high variability of the N and P ions are probably related to vegetation or primary instream processing, with differing geology having little apparent control.

Summary

The development of river composition is reflected in changes in dissolved ion concentrations as water progresses downstream. The composition of the Hoh and Nisqually Rivers develops rapidly during the first few km of travel, a distance relatively unaffected by vegetation, and is fully developed by natural causes before either river departs its respective national park. Concentrations of most dissolved ions increase rapidly from relatively low levels in ice melt to near constant levels in river water.

The comparison of downstream trends for the Hoh and Nisqually rivers, presented here, emphasizes differences in ion concentrations between rivers and their probable geologic controls. Most downstream increases in ion concentrations can be explained by chemical weathering—the processes of hydration, hydrolysis, and hydrogen replacement of cations. Although similar development was observed for both rivers, final

concentrations were, in most cases, decidedly different. Since vegetation is similar between watersheds and human disturbances are small, compositional differences between rivers result primarily from mineralogical differences in underlying bedrock and, with the exception of calcite, reflect the relative resistance to weathering of the Hoh River sediments as compared to the Mt. Rainier volcanics.

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Canada Goose Nesting Performance along the Hanford Reach of the Columbia River, 1971-1981

Abstract
Clutch size observed in 1215 hatched Great Basin Canada Goose (*Branta canadensis mofitti*) nests from 1971-1981 was 5.6. The average percent of successful nests was 82 percent. A mean of 135 nests per year since 1971 is lower than the 215 nests per year observed during 1953-1970. Loss of nesting due to coyote predation on Locke Island—#6 has accounted for the overall drop in number of nests.

Introduction

The Hanford nesting population of the Canada Goose has been studied since 1950. Hanson and Eberhardt (1971) have discussed the 1953-1970 period in great detail. This report examines data collected from 1971 to 1981 and continues a record of an important nesting population of the Great Basin Canada Goose. One of the initial purposes of these studies was to document the reproductive performance of the goose population, and this aspect of the investigation has continued to determine whether nesting performance would demonstrate a delayed response to nuclear reactor operations. Radionuclide content of Canada goose eggs measured after the closure of the production reactors indicated that the radionuclide content of goose eggs taken from deserted nests along the Hanford reach was low and primarily of worldwide fallout origin (Rickard and Sweany 1977).

Continuous documentation of nesting performance also provides a way to evaluate the effect of future industrial uses of Columbia River water and any habitat changes induced by hydroelectric dams and turbine additions up and downstream from the Hanford reach. The proposed establishment of a commercial nuclear power reactor "park" at the Hanford Site to produce electricity for export to the regional power network could also produce a number of environmental changes that could affect the nesting goose population as well as other wildlife populations. A hydroelectric dam across the Hanford reach would inundate the islands upon which the nesting goose population depends. The recent opening of the entire length of the Hanford Reach to public recreational use is another feature that could have deleterious effect on the nesting geese. Sequentially collected data can serve as a way to evaluate the effects of past environmental changes and perhaps to recommend future mitigation practices to help maintain a diminishing wildlife resource in south-central Washington.

Study Area

The Hanford Reach (Figure 1) contains the only free-flowing portion of the Columbia

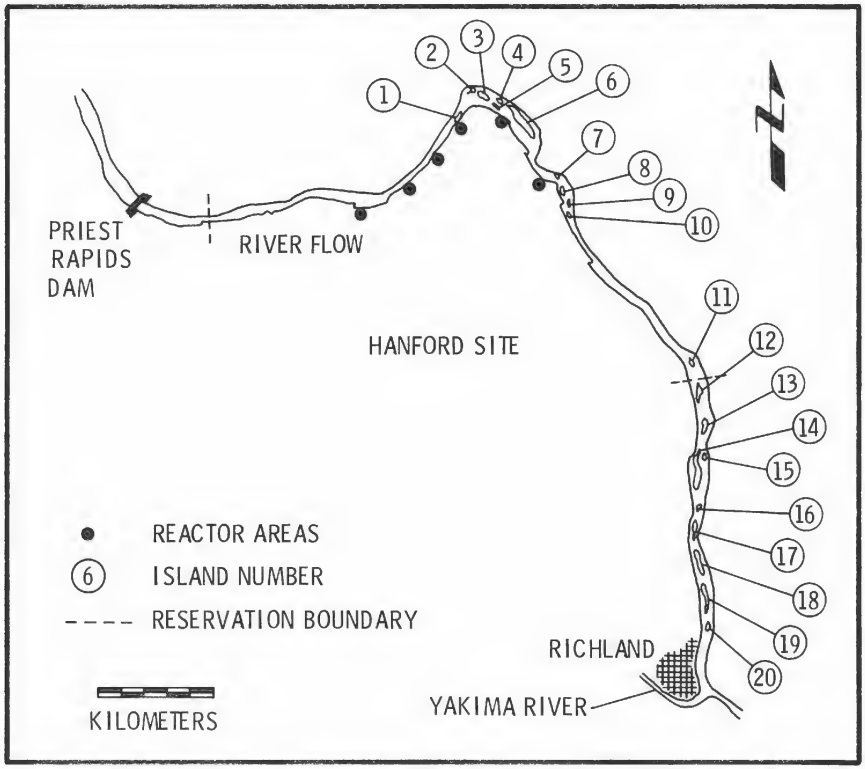

Figure 1. The Hanford reach of the Columbia River, showing locations of 20 islands used for nesting by Canada Geese.

River in the United States upstream from Bonneville Dam. The riparian and aquatic habitats represent relatively unmanaged ecological resources.

Twenty islands provide almost all of the goose nesting habitats along the Hanford Reach (Hanson and Eberhardt 1971). Some of these islands have changed vegetatively since 1970, particularly Islands 18, 19, and 20, as a result of pool elevations of Lake Wallulla, the impoundment created by McNary Dam in 1955. Here the establishment of tree and shrub willows (*Salix* spp, and rank herbaceous species rooted in soil and mud substrates; e.g., reed canary grass (*Phalaris arundinacea*)) have replaced the sparse, short-statured plant communities rooted in cobble stones and gravels which were adapted to the historical seasonal flooding regime and the rapid flows of the free-flowing Columbia River (Fickeisen *et al.* 1980). Locke Island (#6, Fig. 1) has also been grazed by a small resident herd of feral cattle, and Island #13 was burned by human carelessness.

Methods

Nesting surveys during 1971-1981 were conducted biweekly and usually began during the first week of April, as described by Hanson and Eberhardt (1971). Prior to 1971, nesting surveys were conducted weekly, thus not all parameters measured in the earlier

surveys can be compared to the post-1970 data base. We feel, however, that the nest performance parameters we have selected are generally comparable to those of earlier investigations and serve to extend the period of observation an additional 10 years. Certain parameters, such as nesting phenology, nesting success, and fates of eggs, are sensitive to the frequency of observation periods and probably differ slightly from pre-1970 data.

Results and Discussion

The annual number of goose nests on each island can be an effective measure of the changing status of the population. However, other parameters such as nest success, number of eggs laid in successful nests, and average clutch sizes also provide useful information (Table 1) on the reproductive potential. The parameter "nesting success" as we use it, means that a nest was successful if it contained the shells and membranes of hatched eggs, filoplumes from natal down, pipped eggs, or goslings (Hanson and Eberhardt 1971). Average clutch size is the average clutches from all successful nests. We compare productivity data in Table 1 with Hanson and Eberhardt's (1971) figures for the same parameters. In 1215 hatched nests from 1971-1981 we observed a mean clutch size of 5.6. The average percent of successful nests reported by Hanson and Eberhardt was 71 percent, while our value was 82 percent. The generally higher values we report for success probably reflect the biweekly frequency of nest checks. The potential for the goose population to reach the 1958 level is apparently still present based on productivity parameters.

TABLE 1. Productivity of Canada Goose nests on the Hanford Reach of the Columbia River, 1971 to 1980.

Year	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	Avg.
Total nests	112	160	127	146	108	111	125	141	136	156	166	135
Number of successful nests	99	133	116	111	98	100	78	112	113	111	144	110
Percent successful nests	88	83	91	76	91	90	62	79	83	71	87	82
No. of eggs in successful nests	566	741	643	582	528	536	455	644	649	607	883	620
Average clutch size	5.7	5.6	5.5	5.2	5.4	5.4	5.8	5.8	5.7	6.6	6.1	5.6

The number of goose nests established on the Hanford reach islands has fluctuated from year to year, but a general decline in overall numbers is evident. More than 300 goose nests were present in 1958, but in 1975 only 108 nests were counted (Fig. 2). This observed decline in the number of nesting attempts, we believe, is due to a combination of factors, with the common coyote (*Canis latrans*) assigned an important role in the decline. The displacement of a resident human population from the reach of the Columbia in 1943 was initially beneficial to the goose population, by reducing human visitations to the islands. This kind of site management also benefitted the coyote population by providing a release from control measures.

The most dramatic effect of the coyote on the goose population is illustrated for Locke Island (Island #6), which has 106 acres and is the largest of the islands (Fig. 3). In 1957, Locke Island supported at least 129 goose nests (Hanson and Eberhardt 1971). The first evidence of coyote invasion of the island was recorded in 1959, when 42 of 96 nests were destroyed (Hanson and Eberhardt 1971). The second coyote incident

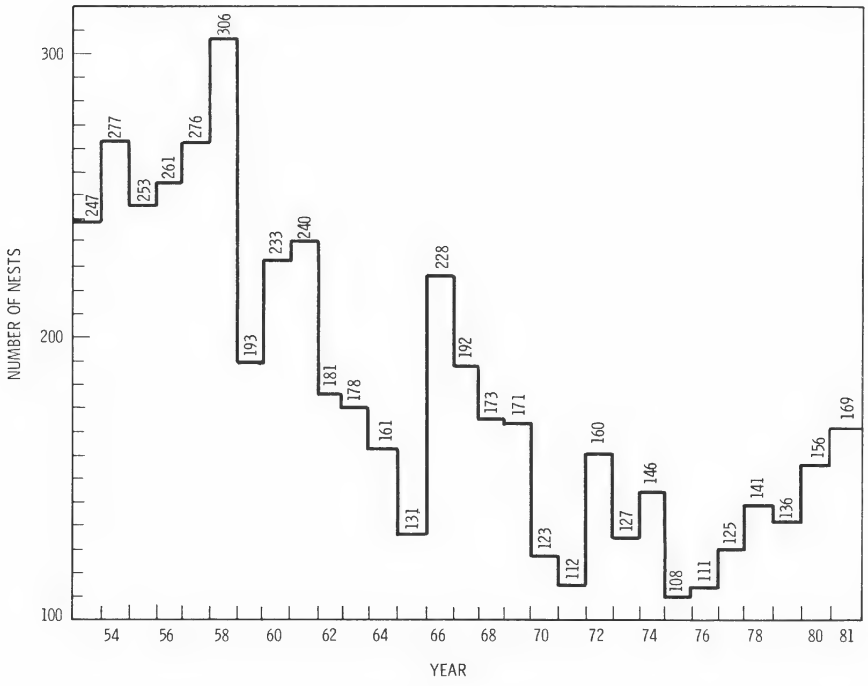

Figure 2. Number of Canada Goose nests found on the Hanford Reach, 1954-1981.

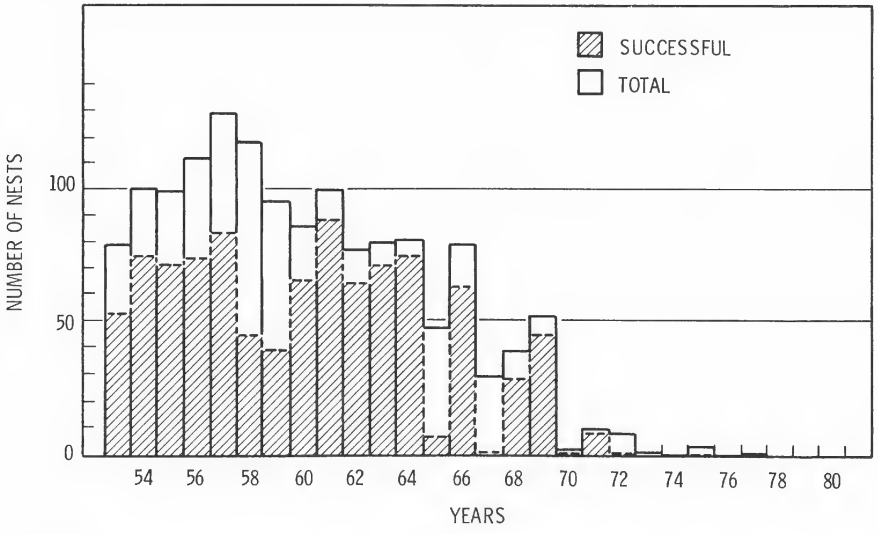

Figure 3. Number of Canada Goose nests established on Island 6 (Locke Island), Hanford Reservation and the number of successful nests, 1953-1981.

occurred in 1965, when a single coyote killed seven geese, destroyed eleven nests, and was probably responsible for the desertion of 28 nests. In the fall of 1966, two coyotes took residence on the island, resulting in the failure of all but one of 27 nests during the 1967 nesting season. In February 1968, two coyotes were shot, and the number of goose nests slightly increased that same year. Since 1970, coyotes have been more or less permanent residents on Locke Island, and coyote removal was not practiced again until 1978. By 1980 the Game Department had killed 159 coyotes along the Hanford Reach (D. Flohr, pers. comm.). Nesting geese are still absent from Locke Island, while coyotes continue to persist. In fact, a family of coyotes has taken up residence on the island despite efforts to control them. Clearly, the survival of this coyote family shows that "general" coyote control is ineffective and that the Locke Island situation emphasizes the importance of individual animals as predators. Hanson and Eberhardt (1971) noted the same predator situation in their study and pointed out that an indiscriminate coyote suppression program conducted during their study provided no increase of the nesting Canada Goose population. Locke Island has also undergone some changes in plant community composition in the past decade by grazing of feral cattle. Cheatgrass (*Bromus tectorum*) now dominates much of the island formerly dominated by native dryland perennial forbs and grasses. These vegetative changes may have had some effect on goose nesting, but the overriding factor has clearly been the presence of coyotes on the island during the nesting season.

To better understand the importance of Locke Island, one need only to examine the total number of nests observed on the Hanford Reach island since 1953. The mean of 135 nests per year since 1971 is lower than 215 nests per year observed during 1953-1970 (Hanson and Eberhardt 1970). This decrease coincides with the near complete termination of nesting on Islands 3, 4, 6, 8, 10, 13, 14 (Dewaard 1981). These islands supported 51 percent of total nests during 1953-1970 but less than 4 percent since 1970. Island 6 supported 37 percent of the total nests prior to 1970 but less than 2 percent since then. DeWaard (1981) analyzed Battelle's data set on Canada Goose nesting performance, eliminating Island 6 in his analysis. He found annual means of 136 (S.E. = 7) and 128 (S.E. = 5) nests per year during 1953-1970 and 1971-1981, respectively. These means were not significantly different ($t = 0.792$, 24 df, $P > 0.40$). Loss of nesting on Island 6 alone clearly accounts for the overall drop in number of nests over the entire study area.

Since the Canada Goose nesting population appears to be fluctuating around 130 nests per year, we can assume that the Hanford islands are supporting the maximum number of nesting geese. The average clutch size and percent successful nests have remained nearly unchanged from the 1953-1970 to 1971-1981 periods, indicating that the local goose population is reproductively healthy. An increase in total production of geese, however, is not expected unless nesting on Island 6 is restored to levels present in the early 1960s.

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Secondary Succession in the Pseudotsuga menziesii/ Physocarpus malvaceus Association

Abstract

The *Pseudotsuga menziesii/Physocarpus malvaceus* association is widespread in the northern Rocky Mountains and has high value for grazing, wildlife, and production of timber. Little is known, however, regarding community composition of successional series. Descriptions and an ordination were made of twenty-seven communities in this association to develop secondary successional sequences.

Sites undisturbed since 1900 had vegetative compositions that generally paralleled published records of climax communities. Burning produced high cover of *Ceanothus sanguineus* Pursh and *Spriaea betulifolia* Pall., whereas logging produced high cover of *Holodiscus discolor* (Pursh) Maxim. and *Rosa gymnocarpa* Nutt. *Rosa nutkana* Presl was the only shrub developing highest cover on grazed areas. In the herbaceous layer, *Calamagrostis rubescens* Buckl. had high cover on burned sites, whereas *Arnica cordifolia* Hook. had high cover on logged areas. Species composition in the herbaceous layer of grazed sites showed the most variability.

The successional sequence cannot be divided into recognizable, discrete stages, but forms a continuum with vertical as well as horizontal direction. Disturbance intensity, apparently, is the most important factor affecting succession and time the least important.

Introduction

Since the Daubenmires' forest classification of northern Idaho and adjacent Washington (1968), all major Idaho and Montana forested areas have been classified based on climax or near-climax communities (Pfister *et al.* 1977; Steele *et al.* 1977, 1981). Most successional communities in the northern Rockies, however, await descriptions. This paper describes successional communities in the *Pseudotsuga menziesii/Physocarpus malvaceus* association following disturbance by logging, fire, and grazing.

The group of vascular plants commonly occurring together and known as the *Physocarpus malvaceus* union is dominated by dense shrubs. *Physocarpus malvaceus* (Greene) Kuntze and *Holodiscus discolor* (Pursh) Maxim. form a nearly continuous layer 1 to 2 meters in height. Beneath this layer, *Rosa gymnocarpa* Nutt., *Spiraea betulifolia* Pall., and *Symphoricarpos albus* (L.) Blake form a low (0.2 to 1 m) shrub layer. Varying amounts of tall (2 to 5 m) shrubs, such as *Salix scouleriana* Barratt, *Amelanchier alnifolia* Nutt., *Acer glabrum* Torr., and *Prunus virginiana* L., occur as isolated individuals rising above the dominant mid-shrub canopy. The herbaceous plant community is characterized by *Calamagrostis rubescens* Buckl., *Carex geyeri* Boott, *Arnica cordifolia* Hook., *Arenaria macrophylla* Hook., and *Osmorhiza chilensis* H. & A. (Daubenmire & Daubenmire 1968; Pfister *et al.* 1977; Steele *et al.* 1976, 1981).

The *Physocarpus malvaceus* union is found in the northern Rockies chiefly at or near

the lower limits of forest development, 500 to 1300 m in elevation. This union is reported throughout northern Idaho and northeastern Washington (Daubenmire & Daubenmire 1968), east to the Continental Divide in Montana (Pfister *et al.* 1977), as far south as northwestern Utah (Henderson *et al.* 1976), and west into the Wallawa and Blue Mountains of northeastern Oregon and southeastern Washington(Franklin & Dyrness 1973).

Throughout the entire area this union occurs primarily in the *Pseudotsuga menziesii/Physocarpus malvaceus* association. In northern Idaho, this association occurs on moderately well-drained soils formed primarily in loess with varying amounts of volcanic ash, pebbles, and cobbles on gentle to moderately steep slopes. It is generally found between the drier *Pinus ponderosa/Festuca idahoensis* or *Pinus ponderosa/Physocarpus malvaceus* associations and the moister *Abies grandis/Pachistima myrsinites* or *Thuja plicata/Pachistima myrsinites* associations.

Importance

The *Pseudotsuga menziesii/Physocarpus malvaceus* association is important to timber production, primarily of *Pseudotsuga menziesii* (Mirbel) Franco. *Pseudotsuga* produces the greatest volume of annual cut in the northern Rocky Mountains (Greene & Setzer 1974). *Pinus ponderosa* Dougl. is the major seral tree on these sites, where it achieves its best volume growth (Barrett 1962).

This association is also important for livestock grazing since it is easily accessible, and because forage production in successful stands of *Pseudotsuga menziesii/Physocarpus malvaceus* is high (Tisdale 1960). Thilenius (1960) demonstrated that common *Physocarpus malvaceus* union shrubs such as *Symphoricorpos albus*, *Holodiscus discolor*, *Physocarpus malvaceus*, and *Spiraea betulifolia* can serve as summer forage. Under heavy grazing pressure, the shrubs diminish and pasture grasses such as *Poa pratensis* L. assume dominance (Daubenmire & Daubenmire 1968).

The*Pseudotsuga menziesii/Physocarpus malvaceus* association is important for wildlife primarily in seral stages where the high shub density provides both winter and summer browse. *Amelanchier alnifolia*, *Ceanothus sanguineus* Pursh, and *Salix scouleriana*, all prominent members of early seral stages, are highly palatable to whitetail deer (*Odocoileus virginianus*), mule deer (*O. hemionus*) and elk (*Cervus canadensis*) (Leege and Hickey 1971, Lyon 1971). In addition, the dense shrubs characteristic of this union provide both visual and thermal cover for deer and elk, and nesting habitat, cover, and food for several nongame animals.

Methods

To ensure that the successional trends would reflect disturbances, environmental variability was kept to a minimum by selecting stands that fell within specified limits. Only northerly exposures were sampled, all having slopes between 30 and 60 percent, between 650 and 990 m elevation, and having relatively deep soils mostly of the Taney silt loam series. These limits allow a certain degree of variation, providing a broad enough base to make the results usable to land managers, while keeping environmental variables reasonably constant.

Twenty-seven sites within the Douglas-fir zone were selected in northern Idaho. Based on owner records, four of these sites had not been disturbed since the early

1900s, five had been logged, three had been burned at least once, four had been grazed, two had been logged and burned, and nine had been logged and grazed. Successional trends would have to be reconstructed from these patterns of disturbance, since fence line/property line contrasts for comparison between disturbed and undisturbed sites could not be found.

Field Methods

Three of the most frequently sampled attributes considered in plant community ecology are density, frequency, and cover. The use of density, however, is related to quadrat size and shape (Bormann 1953, Lindsey 1956), and it is difficult to measure on rhizomatous plants such as grasses, many of which appear in the *Physocarpus malvaceus* union. Frequency, which is the percentage of microplots in which a plant occurs, also depends on quadrat size, but provides a more objective description of the vegetational distribution than does density (Mueller-Dombois & Ellenberg 1974). Crown cover is used to determine species' dominance in a site and has been considered "the most important single parameter of a species in its community relations" (Lindsey 1956).

In this study, a modified version of the line-strip method (Wooden and Lindsey 1954) for estimating cover was used (Fig. 1). Sampling consisted of six transects, each 15 m long and parallel to the contour. Shrub cover was measured to the nearest 0.1 m by shrub crown interception of the vertical plane of the transect line. The herbaceous layer was sampled by a series of thirty-six 2 x 5 dm microplots, situated with the long axis at right angles to the transect line. Cover was estimated for all species, and frequency was calculated for the forbs and grasses. Cover estimates in this study apply only to the herbaceous layer and consisted of the following percentage classes: <1, 1-5, 5-25, 25-50, 50-75, 75-95, and 95-100 percent.

Analysis of Data

Succession is not usually a linear development from early seral communities to climax vegetation. Instead, there may be a number of pathways to a particular climax commu-

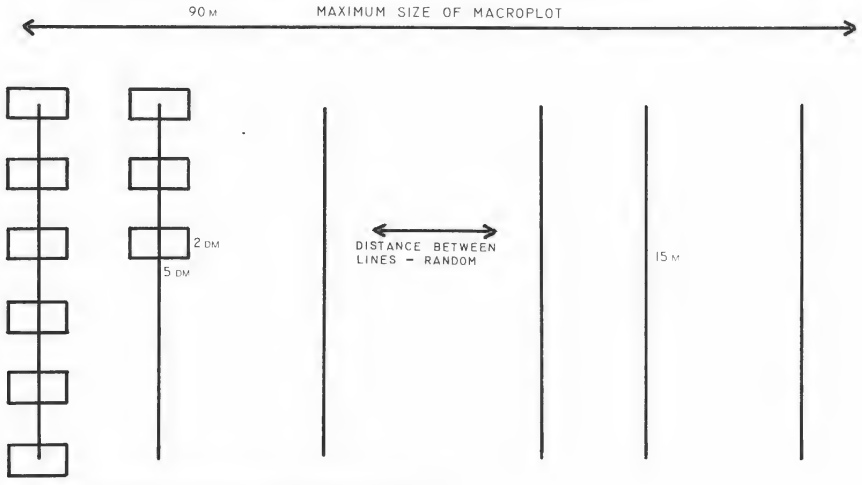

Figure 1. Schematic diagram of sampling method.

nity. Multidimensional ordination techniques are believed to give a better representation of these multipath successions than uni-dimensional techniques (Gauch & Dripps 1973). We used the computerized Cornell Ecology Program No. 4 (Gauch and Dripps 1973) for the Bray-Curtis multidimensional ordination (Bray and Curtis 1957) to plot communities along the successional gradient, as this ordination has been shown to give both statistically and biologically valid results (Gauch and Whittaker 1972). This technique uses either numerical data or simple presence or absence of species and is based on the percent similarity of sample sites. Using the equation percent similarity = $2w/(a + b) \times 100$, "w" represents the number of species common to sites A and B, while "a" and "b" represent the total number of species in sites A and B, respectively.

Results

Climax Communities

In this study, four sites with no record of disturbance since 1900 supported vegetation similar to published descriptions of climax communities (Daubenmire and Daubenmire 1968; Steele *et al.* 1976, 1981). At these sites, *Physocarpus malvaceus* was the dominant shrub, comprising 68 percent of the shrub cover, followed by *Symphoricarpos albus*, *Holodiscus discolor*, and *Rubus parviflorus* Nutt., all with coverage under 10 percent (Table 1). The herbaceous layer (Table 2) of these undisturbed sites did not differ greatly in general composition from the published descriptions of climax conditions, with one exception. Contrary to the data of most observers (Daubenmire and Daubenmire 1968; Steel *et al.* 1976, 1981), coverage of *Smilacina stellata* (L.) Desf. tended to increase from highly disturbed to undisturbed sites, where its coverage in this study was twice that of *S. racemosa* (L.) Desf. From these data, it appears that *S. stellata* is the more shade-tolerant species. *S. stellata* is also an indicator of moister conditions as indicated by its high constancy in the moist *Pachistima myrsinites* union.

These four undisturbed sites, characteristic of the *Pseudotsuga menziesii/Physocarpus malvaceus* association, were used as endpoints in the successional model.

Logged and Burned Communities

In the *Physocarpus malvaceus* union, virtually all shrubs are capable of root-sprouting (Leege and Hickey 1971; Lyon 1966, 1971; Whittinger *et al.* 1977) and would be expected to maintain their presence after disturbance by logging or fire. On the undisturbed sites, *Acer glabrum* and *Salix scouleriana* appeared only occasionally but comprised 7 to 22 percent of total shrub cover on sites that had been logged and/or burned (Table 1). *Symphoricarpos albus* averaged only 8 percent cover on the undisturbed sites, whereas its coverage on these logged/burned sites averaged 13 percent. *Rubus parviflorus* occurred with 21 percent average cover on these sites, compared with 8 percent or less on all other sampled areas.

Ceanothus sanquineus and *Spiraea betulifolia* had coverages of 21 percent and 12 percent, respectively, on burned-only sites. Yet on logged-only areas, these two shrubs comprised less than 1.5 percent of the shrub cover. Climax descriptions of northern and central Idaho indicate that *Spiraea betulifolia* increases in importance in the slightly drier and warmer conditions found in the *Pinus ponderosa/Symphoricarpos albus* and *Pseudotsuga menziesii/Symphoricarpos albus* associations. Burning in the *Pseudotsuga menziesii/Physocarpus malvaceus* association, perhaps, is producing environmental conditions sim-

TABLE 1. Percent (constancy) and average percent cover of selected shrubs.

Species	Climax n=4		Burned n=3		Logged n=5		Logged & burned n=2		Grazed n=4		Logged & grazed n=9	
Acer glabrum			(33)	1.8	(40)	1.7						
Amelanchier alnifolia	(50)	.4	(67)	1.4	(100)	4.0					(89)	2.2
Ceanothus sanguineus			(100)	20.8	(40)	1.3	(100)	22.0	(25)	8.4	(22)	.2
Holodiscus discolor	(50)	8.0	(67)	3.9	(80)	21.1	(100)	1.8	(75)	9.4	(78)	9.5
Lonicera ciliosa	(50)	.3			(80)	1.9					(11)	.2
Physocarpus malvaceus	(100)	67.7	(100)	38.3	(100)	37.0	(100)	14.3	(100)	63.0	(100)	67.5
Prunus virginiana	(25)	.2	(100)	5.2	(20)	.4					(22)	3.5
Rosa gymnocarpa	(50)	2.4			(60)	5.1	(100)	.9	(50)	.5	(67)	2.3
Rosa nutkana	(50)	.4	(100)	1.9	(60)	3.5	(100)	1.7	(75)	7.7	(44)	1.3
Rosa woodsii	(75)	.9	(67)	.8	(20)	.8					(56)	.7
Rubus parviflorus	(75)	7.8			(60)	2.1	(100)	21.0			(44)	3.1
Salix scouleriana			(33)	.7	(60)	7.6					(22)	.4
Spiraea betulifolia	(75)	3.5	(100)	11.7	(40)	.9	(100)	.9	(25)	.2	(56)	.8
Symphoricarpos albus	(100)	8.2	(100)	13.2	(100)	12.6	(100)	14.7	(100)	4.6	(100)	6.2
Ave total cover		43.4		89.2		57.4		107.5		54.4		60.3

TABLE 2. Percent (constancy), average percent cover, and percent (frequency) of selected herbaceous species.

Species	Climax n=4			Burned n=3			Logged n=5			Logged & burned n=2			Grazed n=4			Logged & grazed n=9		
Adenocaulon bicolor							(40)	1.2	(8.4)							(11)	.3	(.6)
Anemone piperi	(50)	2.2	(36.1)	(33)	.1	(4.6)	(100)	.2	(12.8)	(50)	.01	(.6)				(56)	.3	(11.6)
Arenaria macrophylla	(100)	5.3	(56.0)	(100)	1.0	(28.7)	(100)	1.4	(38.9)	(100)	.2	(.8)	(100)	3.9	(55.5)	(89)	2.8	(38.0)
Arnica cordifolia	(100)	5.8	(34.7)	(67)	.8	(25.9)	(100)	8.0	(42.2)	(100)	2.0	(43.0)	(100)	4.8	(38.9)	(89)	4.2	(31.8)
Aster conspicuus				(67)	.5	(8.3)	(60)	.3	(5.6)	(100)	2.8	(2.4)				(11)	.1	(.3)
Cerastium vulgatum													(25)	.2	(15.3)	(22)	T	(1.0)
Cirsium arvense				(67)	.3	(8.3)							(25)	.1	(.03)	(78)	.7	(5.6)
Disporum trachycarpum	(50)	.3	(2.8)				(80)	.5	(5.6)							(11)	.01	(.3)
Epilobium angustifolium				(33)	.3	(.9)										(22)	.3	(2.2)
Epilobium sp.				(100)	1.1	(33.3)				(50)	.01	(.6)	(50)	.1	(9.0)	(44)	.03	(5.2)
Galium boreale	(100)	.3	(12.5)	(67)	1.8	(14.8)	(100)	.1	(8.4)	(100)	.1	(.6)	(25)	.03	(.7)	(67)	.1	(8.4)
Heuchera cylindrica				(67)	.1	(3.7)										(11)	T	(.3)
Hieracium albiflorum				(67)	.3	(2.8)	(60)	.1	(3.3)									
Hydrophyllum capitatum	(T)	.03	(.7)													(44)	.1	(4.6)
Hypericum perforatum				(100)	.8	(14.8)				(100)	.9	(16.7)						
Lathyrus bijugatus							(60)	.05	(4.4)				(25)	.03	(2.1)	(44)	.03	(3.7)

TABLE 2. (cont.)

Species	Climax n=4			Burned n=3			Logged n=5			Logged & burned n=2			Grazed n=4			Logged & grazed n=9		
Lithophragma parviflora	(75)	.03	(2.1)							(50)	.02	(.6)	(75)	.01	(4.2)	(44)	.3	(6.5)
Lithospermum ruderale													(25)	.03	(2.1)	(22)	.01	(.6)
Microsteris gracilis (var. gracilis)				(67)	.1	(5.6)							(25)	.03	(2.8)	(56)	.6	(5.6)
Mitella stauropetala							(60)	.1	(2.2)	(50)	.2	(.6)	(25)	.01	(.7)	(33)	.02	(2.5)
Osmorhiza chilensis	(75)	3.2	(29.2)	(33)	.03	(1.8)	(60)	.3	(6.7)	(50)	.02	(.6)	(75)	.1	(5.6)	(44)	.2	(.08)
Potentilla glandulosa				(33)	.01	(.9)	(20)	.1	(.6)	(30)	.2	(.9)	(25)	.01	(1.4)	(56)	.6	(3.7)
Potentilla gracilis													(25)	.03	(.7)	(33)	.1	(2.5)
Prunella vulgaris (var. lanceolata)													(25)	.2	(4.8)	(33)	.3	(6.7)
Rumex acetosella													(50)	.2	(5.6)	(22)	.03	(3.7)
Senecio integerrimus (var. exaltatus)													(25)	.03	(.7)	(44)	.3	(3.1)
Smilacina racemosa	(100)	2.8	(18.0)				(100)	3.2	(16.1)							(56)	.8	(5.8)
Smilacina stellata	(50)	11.0	(5.5)				(100)	1.4	(13.3)				(25)	.03	(.7)	(22)	.02	(.6)
Taraxacum officinale				(33)	.03	(1.8)							(75)	.8	(10.4)	(33)	.1	(5.6)
Thalictrum occidentale	(100)	7.3	(35.4)	(33)	.03	(.9)	(100)	2.0	(16.1)	(50)	.2	(5.6)	(25)	.5	(5.6)	(67)	.6	(5.0)
Agropyron spicatum				(100)	.04	(2.8)												
Bromus tectorum																(33)	.6	(7.0)
Calamagrostis rubescens	(100)	.9	(7.0)	(100)	9.4	(54.5)	(100)	5.8	(25.0)	(50)	1.6	(2.4)	(50)	.1	(4.8)	(33)	.8	(7.4)
Carex geyeri	(75)	5.8	(29.8)	(100)	.2	(13.0)	(100)	4.4	(29.4)				(75)	2.2	(13.9)	(78)	.8	(7.7)
Festuca occidentalis	(50)	.05	(2.8)	(33)	.1	(.9)	(40)	.03	(5.3)	(50)	.1	(.6)	(100)	3.7	(44.5)	(67)	1.2	(12.6)
Poa pratensis	(25)	T	(.7)	(100)	2.8	(21.3)				(100)	.5	(25.0)	(100)	7.4	(48.5)	(78)	3.4	(24.4)
Trisetum canescens				(33)	.01	(.9)				(50)	.01	(.6)				(44)	.1	(5.8)

ilar to those found in the *Pseudotsuga menziesii/Symphoricarpos albus* association. *Ceanothus sanguineus*, while able to root-sprout, also has seeds with the ability to remain dormant in the soil for long periods of time, or until fire produces conditions suitable for germination (Orme and Leege 1976). This ability would explain the greater coverage of *Ceanothus sanguineus* on the burned sites. Burned sites, in general, had higher shrub cover but fewer dominant shrub species than logged sites.

In the herbaceous layer (Table 2), rhizomatous *Agropyron spicatum* (Pursh) Scribn. and Smith (with 3 percent frequency) was the sole species found only on burned sites, while *Epilobium* sp., *Galium boreale* L., *Heuchera cylindrica* Dougl., and *Calamagrostis rubescens* had higher cover and frequency values on burned areas than other sites. *Adenocaulon bicolor* Hook. and *Arnica cordifolia* were found more often on logged-only sites. Species found on sites both burned and logged include *Aster conspicuus* Lidl. and the introduced *Hypericum perforatum* L.

Grazed Communities

Generalizations from grazed sites are difficult because intensity and season of use differ on each site. Some trends in vegetative composition are apparent, however. On grazed sites, *Symphoricarpos albus* and *Spiraea betulifolia* occupied at least 50 percent less crown space than on other sampled sites (Table 1). *Physocarpus malvaceus* and *Holodiscus discolor* had nearly the same coverage in grazed areas as on undisturbed sites. *Rosa nutkana* Presl was the only shrub with a cover higher on grazed sites than on other sampled sites. Average total shrub cover on grazed sites was considerably less than on logged and/or burned areas, suggesting that cattle were foraging on shrubs, as reported by Thilenius (1960).

Species composition in the herbaceous layer (Table 2) of grazed-only sites showed the most difference when compared to undisturbed areas. This difference would be expected, since cattle are primarily grazers. There were several species that had much lower cover and frequency on these grazed sites, notably *Osmorhiza chilensis, Calamagrostis rubescens,* and *Carex geyeri.* Species that tended to be more abundant on grazed areas included *Lithospermum ruderale* Dougl., *Festuca occidentalis* Hook., *Poa pratensis*, *Cerastium vulgatum* L., *Rumex acetosella* L., and *Taraxacum officinale* Weber.

Logged and Grazed Communities

Sites that had been disturbed by both logging and grazing were classed into two groups: 1) grazed prior to logging (GL), 7 sites; and 2) grazed after logging (LG), 2 sites. Essentially, there was no difference in the total shrub cover (Table 1) between these two groups. *Physocarpus malvaceus* dominated the sites, with other species relatively low in cover. The coverage of *Spiraea betulifolia, Symphoricarpos albus, Holodiscus discolor,* and *Rosa nutkana* was twice as high on the GL sites as on the LG sites. In addition, *Rubus parviflorus* was found on GL sites but not LG, while *Crataegus douglasii* Lindl. occurred on LG sites.

The herbaceous layer (Table 2) of these logged/grazed communities contained high numbers of species which either did not occur in the other sampled sites or occurred with low cover and frequency. Such species include *Cirsium vulgare* (Savi) Tenore, *Epilobium angustifolium* L., *Hydrophyllum capitatum* Dougl., *Prunella vulgaris* L., *Senecio integerrimus* Nutt., and *Bromus tectorum* L.

On GL sites *Epilobium angustifolium, Potentilla glandulosa* Lindl., *Senecio integer-*

rimus, *Trisetum canescens* Buckl., *Bromus tectorum*, and *Cirsium vulgare* occurred with both higher cover and frequency than on the LG sites. Conversely, on LG sites *Epilobium* sp., *Hydrophyllum capitatum*, *Lithophragma parviflora* (Hook.) Nutt., *Prunella vulgaris*, *Poa pratensis*, and *Phleum pratense* L. had higher cover and frequency than on GL sites.

Ordination

A three-dimensional ordination (Bray and Curtis 1957) was made using Sorensen's Index of Similarity (Sorensen 1948) and presence-absence data on 81 species. Ordination end-points based on similarities were chosen according to a method described by Newsome and Dix (1968). Graphically, the results formed a cone-like or pyramid-like model of succession (Fig. 2). The Y-axis of this cone is represented by degree of disturbance, as determined by qualitative observation. Heavily and moderately disturbed sites are near the base and least disturbed near the apex of this successional model. The

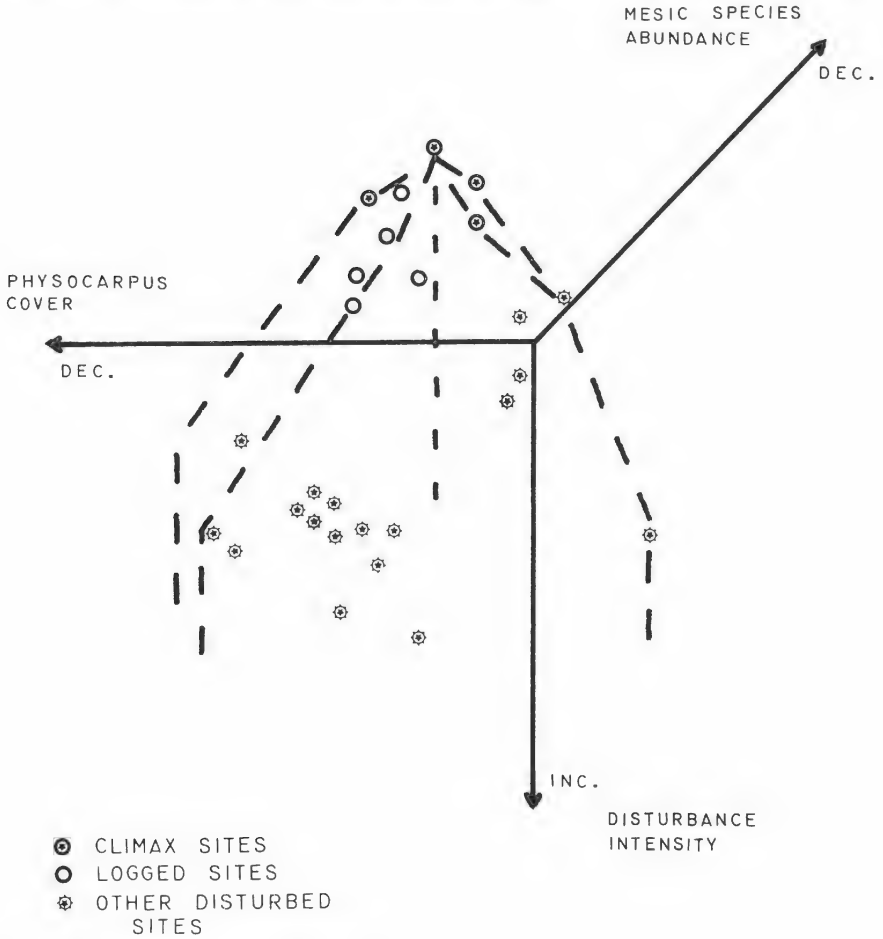

Figure 2. Depiction of ordination results.

X-axis represents *Physocarpus malvaceus* cover, and the Z-axis, although difficult to interpret, appears related to the abundance of mesic species. This cone-like model agrees with that described for a grassland secondary succession (Huschle and Hironaka 1980).

Discussion

Some of the vegetational variability found among sample sites may be attributed to slight differences in soil properties, available moisture, topography, and various other factors. Disturbance patterns and intensities, however, are most likely responsible for the majority of the vegetational variation summarized herein. Species, when subjected to a continual or periodic disturbance, may develop adaptations for successful reproduction. Root sprouting, noted by many researchers (Leege and Hickey 1971; Lyon 1966, 1971; Whittinger *et al.* 1977; and others), was especially noticeable on burned sites, particularly on *Physocarpus malvaceus*, *Holodiscus discolor*, *Ceanothus sanguineus*, and *Acer glabrum*, all important wildlife browse species. Sites that had been logged and burned had the highest average shrub cover, primarily due to the high numbers of root sprouts. Browsing tends to stimulate lateral shoot growth rather than root sprouts, causing an increase in crown volume (Stoddart and Smith 1955) and often an increase in vigor. This was particularly noticeable in the grazed sites sampled in this study.

Disturbance intensity is difficult to measure, yet this factor is undoubtedly important in development of the understory composition. No observations on fire intensity were possible in this study, and only qualitative observations are available for differences in logging and grazing intensities. Nonetheless, the effects of disturbance intensity should be considered an important source of variation in community composition.

The lack of distinct and recognizable successional stages in the ordination of the twenty-seven sampled sites reflects the complexity of secondary succession, and the results suggest a continuum from early seral to climax communities. One expected vegetational trend is the increase in cover of shade-tolerant species from seral to climax and the attendant decrease in cover of shade-intolerant species.

The results of this study also indicate that community composition may not be correlated with absolute time. Sites most dissimilar from climax communities were not necessarily more recently disturbed. It has been shown (Horn 1974) that the rate of change in composition is faster in earlier stages of secondary succession than in later stages. This phenomenon is due in part to the later stages having greater amounts of shade-tolerant species. Thus, the time required for a community to return to climax conditions depends on what the successional stage is. As multiple disturbances are added to the secondary successional picture, complexity increases. Intensity of disturbance apparently is a dominant factor in secondary succession and the most difficult to quantify.

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Responses of Birds to Timber Harvesting along Meadow Edges in Northwestern Oregon

Abstract

Birds responded to a 25 percent removal of tree cover along two meadows in northwestern Oregon. Total densities were lower in clearcuts than in uncut forests adjacent to meadows. Clearcuts favored birds that preferred early successional stages. Bird composition in meadows differed between the sites. Correlations between bird density and habitat variables generally showed the importance of trees and/or snags for forest birds and shrubs for birds that preferred openings.

Introduction

Whitcomb *et al.* (1976) listed values of retaining small habitat reserves: (1) preservation of taxa that can survive in small areas; (2) preservation of unique microhabitats; (3) provision of "stepping stones" between larger reserves; and (4) provision of local educational and recreational benefits. However, small reserves are more vulnerable to human disturbance and natural disasters than larger areas. An important management question is how much disturbance small areas can withstand and still provide wildlife values. This study involved the bird response to timber harvesting along the edges of small meadows, which comprise less than 1 percent of the area in mountains of northwestern Oregon. Meadows are thought to enhance overall forest diversity and are used extensively by birds (Austin and Perry 1979). Study phases were: (1) comparison of relative density, diversity, and equitability of bird species in meadows and adjacent clearcut and forested areas; (2) comparison of bird composition between portions of meadows adjacent to clearcuts and uncut forests; and (3) assessment of the relationships between relative densities of birds and vegetation parameters.

Study Area

Two study sites were selected in the Western Cascades Province of Oregon. The Mt. Horeb (*MH*) site contained a 24 ha (59 ac) meadow, adjacent clearcut, and adjacent forest at an elevation of 1524-m (5000 ft). The Crabtree Lake (*CL*) site consisted of a 6 ha (15 ac) meadow, adjacent clearcut, and adjacent forest at 1037-m (3400 ft) elevation. The *MH* site was located at the summit of a mountain with a predominantly dry, convex ground surface whereas *CL* was wetter and located in a bowl-shaped depression. Clearcutting (11-12 years old) had removed 25 percent of the tree cover along the edges of both meadows. Predominant trees at *MH* were noble fir (*Abies procera*), Douglas-fir (*Pseudotsuga menziesii*), and Alaska yellow cedar (*Chamaecyparis nootkatensis*); and at *CL* were western hemlock (*Tsuga heterophylla*), grand fir (*Abies grandis*), and Douglas-fir.

Methods

Birds were tallied by the sample count method (Anderson 1972) within contiguous circular plots of 15, 20, and 30-m radii along transect lines in the meadow, clearcut, and forest of each study site (Fig. 1). Plot size varied with bird detectability; smaller plots were used where birds were more difficult to detect. Six minutes were spent at

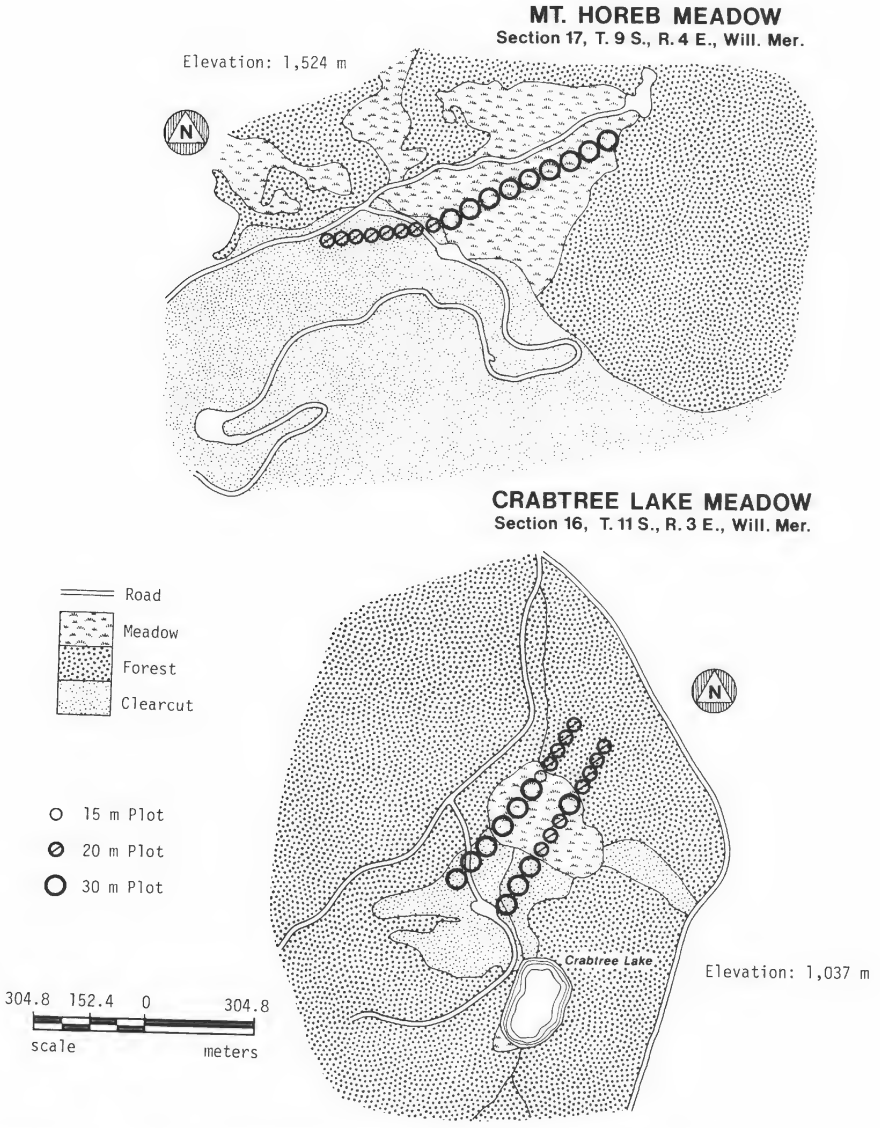

Figure 1. Location of bird census plots at Mt. Horeb and Crabtree Lake Meadows.

each plot and all birds seen or heard within the plots were counted. Censusing was conducted on seven days at each site between 13 May and 24 June from 0530 to 1000.

Vegetation plots were centered within each bird census plot. Trees (>10 cm diameter at breast height) were counted and slash estimated to the nearest 5 percent ground coverage within circular plots of 7.8-m radii. Shrubs in three height classes (0.5-2 m, 2.1-4.5 m, 4.5 m+) were counted within circular plots of 2.2-m radii.

Species diversity was calculated as $H = -p_i \log p_i$, where p_i is the proportion of individuals in the i^{th} species (Shannon and Weaver 1948). Equitability was calculated as $J = H/H_{max}$. The F test and Student Neuman-Keuls test (Zar 1974) evaluated differences in relative density, diversity, and equitability among clearcut, meadow, and forested habitats. The t test assessed differences in relative density, diversity, and equitability between portions of meadows adjacent to clearcuts and uncut forests. Stepwise multiple regression identified relationships between relative density and vegetation parameters. A significance level of $P = 0.05$ was used in all tests.

Results

Relative densities of 31 species observed in clearcut, meadow, and forested areas ranged from 0.1 to 6.3/ha at *MH* and from 0.1 to 5.9/ha at *CL* (Table 1). At *MH*, total density and densities of the Chestnut-Backed Chickadee (See Table 1 for scientific names of birds), Golden-Crowned Kinglet, Black-Throated Gray Warbler, and Hermit

TABLE 1. Density means (N/ha) of bird species within clearcut (CC), meadow (M), and forest (F) at Mt. Horeb and Crabtree Lake study areas, summer 1981.

Bird species	Mt. Horeb			Crabtree		
	CC	M	F	CC	M	F
Vaux's swift (**Chaetura vauxi**)	—	—	—	0.3	2.1	0.8
Rufous hummingbird (**Selasphorus rufus**)	—	—	—	0.7	0.8	—
Hairy woodpecker (**Dendrocopos villosus**)	—	—	0.2	—	0.1	—
Willow flycatcher (**Empidonax traillii**)	0.7	0.1	—	0.1	0.8	—
Western flycatcher (**Empidonax difficilis**)	—	—	—	—	—	2.3
Violet-green swallow (**Tachycineta thalassina**)	—	0.1	—	—	—	—
Gray jay (**Perisoreus canadensis**)	—	—	—	—	0.2	—
Steller's jay (**Cyanocitta stelleri**)	—	—	—	0.2	0.1	0.4
Chestnut-backed chickadee (**Parus rufescens**)	—	—	0.6	—	0.1	1.3
Red-breasted nuthatch (**Sitta canadensis**)	—	—	0.5	—	—	0.3
Brown creeper (**Certhia familiaris**)	—	—	0.2	—	—	—
Winter wren (**Troglodytes troglodytes**)	—	—	—	—	—	0.5
American robin (**Turdus migratorius**)	—	0.2	—	0.3	0.8	0.3
Varied thrush (**Ixoreus naevius**)	—	—	—	—	—	0.1
Swainson's thrush (**Catharus ustulatus**)	—	—	—	**0.6**	**0.1**	**0.1**
Townsend's solitaire (**Myadestes townsendi**)	—	—	0.2	—	—	—
Golden-crowned kinglet (**Regulus satrapa**)	—	0.1	6.3	—	—	5.9
Orange-crowned warbler (**Vermivora celata**)	—	—	0.2	—	—	—
Yellow-rumped warbler (**Dendroica coronata**)	—	0.7	—	—	—	—
Black-throated gray warbler (**Dendroica nigrescens**)	—	—	2.3	—	—	0.3
Hermit warbler (**Dendroica occidentalis**)	—	—	1.9	—	—	0.5
MacGillivary's warbler (**Oporornis tolmiei**)	0.3	0.1	—	0.5	0.2	0.1
Wilson's warbler (**Wilsonia pusilla**)	0.1	0.1	0.2	0.5	0.1	0.8
Red-winged blackbird (**Agelaius phoeniceus**)	—	—	—	—	1.8	—
Pine siskin (**Carduelis pinus**)	—	—	0.2	—	—	—
American goldfinch (**Carduelis tristis**)	—	0.3	—	—	—	—
Rufous-sided towhee (**Pipilo erythrophthalmus**)	0.1	—	—	—	—	—
Dark-eyed junco (**Junco hyemalis**)	1.0	0.7	2.6	0.8	0.1	0.1
White-crowned sparrow (**Zonotrichia leucophrys**)	1.1	0.8	—	—	—	—
Lincoln's sparrow (**Melospiza lincolnii**)	—	—	—	—	1.0	—
Song sparrow (**Melospiza melodia**)	0.7	0.4	—	1.2	2.1	0.4

TABLE 2. F values for comparison of relative bird density, species diversity, and equitability between clearcut (CC), meadow (M), and forest (F) at Mt. Horeb and Crabtree Lake study areas, summer 1981.

Study area	Total density	Vaux's swift	Rufous hummingbird	Willow flycatcher	Western flycatcher	Chestnut-backed chickadee	Red-breasted nuthatch	American robin	Golden-crowned kinglet	Yellow-rumped warbler	Bl.-thr. gray warbler	Hermit warbler	Wilson's warbler	Red-winged blackbird	American goldfinch	Dark-eyed junco	White-crowned sparrow	Lincoln's sparrow	Song sparrow	Species diversity	Equitability
Mt. Horeb	13.5[a]	—	3.8[b]	4.8[b]	—	4.5[a]	1.2	—	26.2[a]	4.4[c]	16.9[a]	28.0[a]	0.1	—	0.8	1.3	2.3	—	1.5	0.5	1.9
Crabtree Lake	3.6[d]	1.6	3.3	3.1	6.7[a]	6.1[a]	—	2.2	34.8[a]	—	—	—	2.6	2.0	—	2.9	—	3.2	3.6[e]	0.8	0.6

[a] $\overline{X}_F > \overline{X}_M$; $\overline{X}_F > \overline{X}_{CC}$

[b] $\overline{X}_{CC} > \overline{X}_F$; $\overline{X}_{CC} > \overline{X}_M$

[c] $\overline{X}_M > \overline{X}_{CC}$; $\overline{X}_M > \overline{X}_F$

[d] $\overline{X}_M > \overline{X}_{CC}$; $\overline{X}_F > \overline{X}_{CC}$

[e] $\overline{X}_M > \overline{X}_F$

Warbler were significantly greater in the forest than in the meadow or clearcut (Table 2). The Rufous Hummingbird and Willow Flycatcher were more abundant in the clearcut than in the forest or meadow, and the Yellow-Rumped Warbler was more common in the meadow than in the clearcut or forest. At *CL*, total density was higher in the forest and meadow than in the clearcut. The Western Flycatcher, Chestnut-Backed Chickadee, and Golden-Crowned Kinglet were more abundant in the forest than in the meadow or clearcut, and the Song Sparrow was more abundant in the meadow than in the forest. Species diversity and equitability were not significantly different among the three habitats in either study area.

The effects of clearcutting on bird composition within the meadows were evaluated by dividing meadow plots into two categories, the meadow edge adjacent to the clearcut (MEC), and the meadow edge adjacent to the forest (MEF). The hypothesis was that relative density, diversity, and equitability would not significantly differ between the two areas if clearcutting along the meadow edge had no effect on avifauna. At *MH*, total density, Yellow-Rumped Warbler numbers, and Song Sparrow numbers were greater in the MEC than MEF (Table 3). No significant differences between relative bird densities in the MEC and MEF were observed at *CL*. Species diversity and equitability were not significantly different between the MEC and MEF in either study area.

TABLE 3. Values of the t statistic for comparison of relative bird density, species diversity, and equitability between meadow edge along clearcut (MEC) and meadow edge along forest (MEF) at Mt. Horeb and Crabtree Lake study areas, summer 1981.[a]

Study area	Total density	Vaux's swift[a]	Rufous hummingbird[a]	Willow flycatcher[a]	American robin[a]	Yellow-rumped warbler[a]	Wilson's warbler[a]	Red-winged blackbird[a]	American goldfinch[a]	Dark-eyed junco[a]	White-crowned sparrow[a]	Lincoln's sparrow[a]	Song sparrow[a]	Species diversity[b]	Equitability[b]
Mt. Horeb	2.3[c]	—	—	—	1.4	2.9[c]	1.0	—	1.0	0.3	1.9	—	2.3[c]	2.4	1.0
Crabtree Lake	0.9	1.9	1.3	1.0	0.6	—	—	1.8	—	—	—	0.9	0.5	0.6	0.6

[a]MEC=28 plots (4 plots replicated 7 times)
MEF=28 plots (4 plots replicated 7 times)
[b]MEC=4 plots
MEF=4 plots
[c]$\bar{X}_{MEC} > \bar{X}_{MEF}$

Bird Densities and Habitat Parameters

The habitat characteristics of the two sites (Table 4) were correlated with bird abundance. The Willow Flycatcher was positively correlated with low, medium, and tall shrub heights and negatively correlated with live trees (Table 5). The Chestnut-Backed Chickadee was positively associated with medium and tall shrub heights and negatively associated with the number of snags. The Red-Breasted Nuthatch was positively correlated with number of snags, the Golden-Crowned Kinglet with live trees, the Black-Throated Gray Warbler with live trees and snags, the Hermit Warbler with live trees, and the Song Sparrow with medium shrub heights. Total bird density was correlated with medium and tall shrub heights, and live trees.

Discussion

At both study areas, total bird density was greater in the forest than in the clearcut, which indicated a negative effect of clearcutting on the bird community overall. Previous studies (listed in Franzreb 1977:22) have reported higher species numbers in older than in younger successional stages of forests, which relates to increased structural diversity (e.g., foliage volume and height) of older stages and a corresponding in-

TABLE 4. Density means of habitat parameters within clearcut, meadow, and forest at Crabtree Lake and Mt. Horeb study areas.

Study site	Habitat parameter	Density means by habitat type		
		Clearcut	Meadow	Forest
Crabtree Lake	Shrubs 0.3-2 m[a]	100,899	71,000	47,846
	Shrubs 2.1-4.5 m[a]	444	6,200	1,231
	Shrubs > 4.5 m[a]	0	400	385
	Trees[a]	111	0	5,769
	Snags[a]	0	0	923
	Slash[b]	15	0	0
	n	6	8	8
Mt. Horeb	Shrubs 0.3-2 m[a]	76,000	14,764	61,155
	Shrubs 2.1-4.5 m[a]	1,250	457	98
	Shrubs > 4.5 m[a]	0	0	196
	Trees[a]	66	0	477
	Snags[a]	0	0	38
	Slash[b]	6	1	0
	n	8	9	7
Combined	Shrubs 0.3-2 m[a]	88,445	42,882	54,501
	Shrubs 2.1-4.5 m[a]	847	3,329	665
	Shrubs > 4.5 m[a]	0	200	291
	Trees[a]	89	0	3,123
	Snags[a]	0	0	481
	Slash[b]	10	1	0

[a]Stems/ha rounded to nearest whole number.

[b]Percent of slash covering ground rounded to nearest whole number.

TABLE 5. Standardized coefficients (x 10^2) from stepwise regression analysis for bird species. All variables are significant ($P < 0.05$, $N = 46$).

Selected habitat parameters[a]	Willow flycatcher	Chestnut-backed chickadee	Red-breasted nuthatch	Golden-crowned kinglet	Black-throated gray warbler	Hermit warbler	Song sparrow	Total bird density
SHB1	+50							
SHB2	+38	+73					+53	+37
SHB3	+30	+35						+39
NTR	-40			+67	+44	+56		+35
NS		-23	+59		+51			
R^2	.64	.66	.35	.45	.63	.31	.28	.46

[a]SHB1 = number of conifer and hardwood stems < 10 cm dbh, 0.3-2 m tall.
SHB2 = number of conifer and hardwood stems < 10 cm dbh, 2.1-4.5 m tall.
SHB3 = number of conifer and hardwood stems < 10 cm dbh, > 4.5 m tall.
NTR = number of conifer and hardwood tree stems > 10 cm dbh.
NS = number of snags > 10 cm dbh.

crease in the number of niches available for birds. Species preferring the forest included the foliage-gleaning Chestnut-Backed Chickadee, Golden-Crowned Kinglet, Black-Throated Gray Warbler, and the Western Flycatcher, an insect hawker and gleaner. Replacement of forest birds by species preferring open habitat was evident in clearcuts at both sites. Similar changes in species composition after clearcutting have been previously reported (Hager 1960, Szaro and Balda 1979). The preference of the Willow Flycatcher for the clearcut at *MH* likely related to their known affinity for shrubby sites (Thomas 1979). Significantly higher numbers of Rufous Hummingbirds in the clearcut at *MH* (mean density was also higher in the clearcut at *CL*) probably related to their preference for nectar-producing flowers (USDA Forest Service 1981) found abundantly in clearcuts. The preference of Song Sparrows for meadow habitat at *CL* rather than at *MH* apparently related to the greater density of shrubs between 2.1-4.5 m tall (Table 4). The preference of Yellow-Rumped Warblers for the meadow habitat at *MH* may have related to their apparent affinity for high elevation meadows in addition to coniferous forests (Thomas 1979).

Comparison of bird density, diversity, and equitability between the MEC and MEF suggested that tree removal had little effect on bird composition at *CL*. However, the meadow was small and the effects of clearcutting may have been ameliorated by use of the meadow by birds from adjacent habitats. Significantly higher densities of all birds, Yellow-Rumped Warblers, and Song Sparrows in the MEC than in the MEF at *MH* could have reflected clearcutting. However, vegetative differences (e.g., shrub density) between the MEC ($\bar{x} = 26{,}500$ stems/ha) and MEF ($\bar{x} = 8800$ stems/ha) may also have affected bird composition. The importance of vegetative density to birds within meadows has been previously reported (Austin and Perry 1979).

Correlations of bird density and habitat variables generally show the importance of tree and/or snag cover for forest birds (e.g., Red-Breasted Nuthatch, Golden-Crowned Kinglet, Black-Throated Gray Warbler, and Hermit Warbler). Shrub cover was important for birds that preferred openings (e.g., Willow Flycatcher and Song Sparrow). Positive correlations between Chestnut-Backed Chickadees and shrubs may relate to their use of shrubs for foraging, especially when conifers are nearby (Thomas 1979, USDA Forest Service 1981).

Conclusions

Clearcutting of coniferous forests adjacent to meadows resulted in replacement of forest birds by those preferring early successional stages, although overall bird densities were lower in clearcuts than in forested habitat. Removal of tree cover along meadow edges had no apparent effect on bird composition within the meadow at one site. However, at another site, higher bird densities in the MEC than in the MEF may have reflected the effects of clearcutting or existing vegetative differences between the MEC and MEF.

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Nest Inhabitants and Ectoparasites of Northern Flying Squirrels, Glaucomys sabrinus (Shaw), from Northeastern Oregon

Abstract

Two species of laelapid mites, *Haemogamasus reidi* and *Echinonyssus* sp. (near *cynomys*), along with an apparently undescribed species of glycyphagid, were the most abundant organisms in nests of the northern flying squirrel (*Glaucomys sabrinus* (Shaw)), in northeastern Oregon. A flea, *Opisodasys vesperalis*, the species of *Echinonyssus* mentioned above, and a species of Acaridae (near *Acotyledon paradoxa*) were the most abundant organisms on the squirrels. Of the 29 taxa found on the squirrels, 15 were also found in the nests. Forms found in the nests but not on the squirrels included laelapid mites of two species: cheyletid mites, including a new genus and two new species, one in the genus *Eucheyletia* (both are being described by Smiley and Whitaker): one glycyphagid mite; fleas of three species; argastid (soft) ticks; and several miscellaneous insects and other invertebrates. Forms found on squirrels but not in nests included six species of fleas, four species of chiggers, and *Dermacarus* sp.

Introduction

There is relatively little information available concerning arthropods that inhabit nests of mammals, and there has been no systematic study dealing with nest inhabitants of the northern flying squirrel (*Glaucomys sabrinus* (Shaw)). The ectoparasites of flying squirrels are also inadequately known (Whitaker and Wilson 1974), but Day and Benton (1980) have studied flea populations of the southern flying squirrel (*Glaucomys volans* (Linnaeus)).

The objective of the present study was to determine the invertebrates associated with the nests of northern flying squirrels in Umatilla, Union, and Wallowa counties, northeastern Oregon, and to compare the results with ectoparasites on flying squirrels from the same area—some from the same nests.

Methods and Materials

Flying squirrels and nests were collected from kestrel nest boxes from March through July. Nest materials and the squirrels' fur were examined for invertebrates under a

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dissecting microscope. Invertebrates were cleared and stained in Nesbitt's Solution containing acid fuchsin. They were mounted in Hoyer's Solution and coverslips were ringed with euparal.

Results

Twenty-nine nests were examined (Table 1). The major nest inhabitants were a species of laelapid mite, *Haemogamasus reidi*, and a species of glycyphagid mite, probably new. The third most abundant form was another species of laelapid mite, *Echinonyssus*, near *E. cynomys*, also probably new. A mite, *Dermanyssus gallinoides*, normally associated with birds was the fourth most abundant nest inhabitant. Its occurrence is not illogical, however, because the squirrels were nesting in boxes normally used by birds, and because the squirrels often nest in tree cavities used by birds.

TABLE 1. Inhabitants of 29 nests of northern flying squirrels (**Glaucomys sabrinus**) and associates of the fur of 31 northern flying squirrels (46 squirrels were examined for fleas) taken from March through July in Umatilla, Union, Wallowa counties, Oregon.

	Nest inhabitants				Squirrel associates			
Names of organism	No. of organisms		Occurrence in nests		No. of organisms		Occurrence on squirrels	
Siphonaptera (Fleas)								
Opisodasys vesperalis (Jordon)	74	2.60	13	44.8	619	13.45	46	100.0
Orchopeas caedens caedens (Jordan)	14	0.48	4	13.8	9	0.20	8	17.4
Megarthroglossus divisus Jordon	8	0.28	4	13.8	4	0.09	3	6.5
Ceratophyllus niger C. Fox	6	0.21	1	3.4	—	—	—	—
Catallagia decipiens Rothschild	1	0.03	1	3.4	—	—	—	—
Tarsopsylla octodecimdentata coloradensis (Baker)	1	0.03	1	3.4	—	—	—	—
Delotelis hollandi Smit	—	—	—	—	2	0.04	1	2.2
Hystrichopsylla o. occidentalis Holland	—	—	—	—	2	0.04	1	2.2
Orchopeas sexdentatus spp. (Baker)	—	—	—	—	2	0.04	1	2.2
Callisopsyllus terinus (Rothschild)	—	—	—	—	1	0.02	1	2.2
Monopsyllus cyrturus (Jordan)	—	—	—	—	1	0.02	1	2.2
Orchopeas caedens durus (Jordan)	—	—	—	—	1	0.02	1	2.2
Flea larvae	67	2.30	13	44.8	—	—	—	—
Anoplura (sucking lice)								
Neohaematopinus sciuropteri (Osborn)	2	0.07	2	6.9	76	2.50	9	29.0
Hoplopleura trispinosa (Kellogg & Ferris)	1	0.03	1	3.4	22	0.71	3	9.7
Microphthirus uncinatus (Ferris)	—	—	—	—	2	0.06	2	6.5
Mallophaga, unidentified (biting lice)	1	0.03	1	3.4	1	0.03	1	3.2
Acarina (mites and ticks) Laelapidae								
Haemogamasus reidi Ewing	1282	44.20	20	68.9	27	0.90	9	29.0
Echinonyssus (near) **cynomys** (Radford)	593	20.70	20	68.9	253	8.20	14	45.2
Haemogamasus pontiger (Berlese)	48	1.70	3	10.3	—	—	—	—
Androlaelaps casalis (Berlese)	1	0.03	1	3.4	—	—	—	—
Androlaelaps fahrenholzi (Berlese)	1	0.03	1	3.4	4	0.13	3	9.7
Echinonyssus longichelae Allred & Beck	—	—	—	—	1	0.03	1	3.2
Glycyphagidae								
Glycyphagid, unidentified, probably new	975	33.60	12	41.4	1	0.03	1	3.2
Gohieria n.sp.	18	0.62	6	20.7	—	—	—	—
Dermacarus tamiasciuri Rupes, Yunker & Wilson	—	—	—	—	8	0.26	1	3.2
Dermanyssidae								
Dermanyssus gallinoides Moss	83	2.90	9	31.0	12	0.39	3	9.7
Cheyletidae								
new gen., n. sp.	67	2.30	11	37.9	—	—	—	—
Eucheyletia n. sp.	4	0.14	1	3.4	—	—	—	—

TABLE 1. (Continued)

Acaridae								
Acotyledon (near) **paradoxa** Oudemans	2	0.07	2	6.9	145	4.70	4	12.9
Myianoetus sp.	1	0.03	1	3.4	—	—	—	—
Trombiculidae								
Euschoengastia oregonensis (Ewing)	—	—	—	—	6	0.19	3	9.7
Neotrombicula microti (Ewing)	—	—	—	—	5	0.16	3	9.7
Euschoengastia peromysci (Ewing)	—	—	—	—	3	0.10	2	6.5
Euschoengastia sciuricola (Ewing)	—	—	—	—	1	0.03	1	3.2
Other mites								
Suborder								
Oribatida	15	0.52	6	20.7	2	0.06	1	3.2
Chortoglyphidae	2	0.07	2	6.9	2	0.06	1	3.2
Caloglyphus sp.	1	0.03	1	3.4	—	—	—	—
Proctolaelaps sp.	—	—	—	—	1	0.03	1	3.2
Miscellaneous unidentified	11	0.38	7	24.1	—	—	—	—
Ixodidia (ticks)								
Argasidae (soft-backed ticks)	2	0.07	2	6.9	—	—	—	—
Ixodes angustus Neumann	2	0.07	2	6.9	3	0.10	3	9.7
Miscellaneous non-parasitic invertebrates								
Collembola (springtails)	4	0.14	2	6.9	—	—	—	—
Diptera (flies)	2	0.07	2	6.9	—	—	—	—
Formicidae (ants)	2	0.07	2	6.9	—	—	—	—
Thysanoptera (thrips)	2	0.07	1	3.4	—	—	—	—
Homoptera (hoppers)	1	0.03	1	3.4	—	—	—	—
Unidentified insects	3	0.10	1	3.4	—	—	—	—
Unidentified arachnids	2	0.07	2	6.9	—	—	—	—

The fifth most abundant nest inhabitant was a flea, *Opisodasys vesperalis*, a characteristic parasite of flying squirrels in western North America (Hubbard 1947). Of the 67 flea larvae found, the majority was probably of this species. Cheyletid n. gen., n. sp., and *Haemogamasus pontiger* were seventh and eighth in abundance.

Gohieria (Glycyphagidae), the ninth most abundant nest organism, was represented by 5 adult females and 13 tritonymphs. This genus is poorly known, although *Gohieria fusca* (Oudemans 1903) was described long ago. *Gohieria fusca* occurs in stored food, a habitat similar to that of nests. Volgin (1961) described *G. longiseta* and *G. orientalis* from the European flying squirrel, *Pteromys volans* (Linnaeus). Finding *Gohieria* on both genera of flying squirrels, *Pteromys* and *Glaucomys*, could indicate an evolutionary relationship between these genera.

The remaining nest-inhabiting arthropods occurred in small numbers. They included several species of mites, ticks, lice (Anoplura), springtails (Collembola), thrips (Thysanoptera), ants (Formicidae), flies (Diptera), and fleas. Two of the three lice were *Neohaematopinus sciuropteri*, a host-specific species of *Glaucomys*.

Thirty-five categories of organisms were found in the nests; they totaled 3299 individuals, or 113.8 per nest. The three most abundant species, however, were mites. Mites comprised 2850, or 86.4 percent of all the individual organisms.

Twenty-nine species of organisms were found on the 31 flying squirrels examined (Table 1). They totaled 1216 individuals, or 41.9 per host individual. The most abundant were the fleas, *Opisodasys vesperalis* (619 individuals), and the mites, *Echinonyssus* near *cynomys* (253 individuals). Acarids, near *Acotyledon paradoxa*, were the third most abundant form (145 individuals). Fourth was the flying squirrel louse, *Neohaematopinus sciuropteri*; 76 individuals (2.5 per squirrel) were found on 29 percent of the squirrels. Twenty-two individuals (0.71 per squirrel) of another louse, *Hoplopleura trispinosa*, were also present on 9.7 percent of the hosts. Twenty-seven

individuals of *Haemogamasus reidi*, 2 oribatids, 2 chortoglyphids, 1 glycyphagid, 3 *Ixodes angustus*, 3 *Androlaelaps fahrenholzi*, 12 *Dermanyssus gallinoides*, 1 mallophagan, and fleas, were all forms that were also found in the nests.

The following 14 taxa were found on the squirrels but not in the nests: 6 species of fleas—*Delotelis hollandi, Hystrichopsylla occidentalis, Orchopeas sexdentatus* ssp., *Callisopsyllus terinus, Monopsyllus cyturus, Orchopeas caedens durus* (1 or 2 individuals each); the mite *Dermacarus tamiasciuri* (8 individuals, 0.3 per squirrel, on 1 squirrel); 4 species of chiggers—*Euschoengastia oregonensis* (6 individuals on 3 squirrels), *Neotrombicula microti* (5 individuals on 3 squirrels), *Euschoengastia peromysci* (3 individuals on 2 squirrels), *Euschoengastia sciuricola* (1 individual on 1 squirrel): *Microphthirius uncinatus* (2 individuals on 2 squirrels); and 1 specimen each of *Echinonyssus longichelae* and *Proctolaelaps* species.

Thus, in general, the major associates of the squirrels were similar to the major nest organisms. Of the 29 taxa found on the squirrels, 15 were also found in the nests.

Forms found in the nests but not on the squirrels (at least in numbers greater than one) were argasid ticks, glycyphagids, and cheyletid mites. Argasid or soft ticks move onto a host to take blood meals, but only for short periods, thus explaining their absence on the squirrels. The cheyletid mites apparently are predators. Adult glycyphagid mites normally remain in the nest, whereas their hypopi use a host for transportation, as was the situation we found. Although a few lice were found in the nests, they were more abundant on the squirrels, because lice attach themselves firmly to a host and often remain in place for long periods. The various insects found in the nests would not be expected to occur on the squirrels.

Chiggers and hypopi of *Dermacarus* were on the squirrels but not in the nests, probably because they, too, form relatively long-term attachments to a host.

Mites previously reported from northern flying squirrels were *Haemogamasus ambulans, H. reidi, Echinonyssus occidentalis*, and *Laelaps kochi* (Allred and Beck 1966, Keegan 1951, Redington 1970, Scholten *et al.* 1962, Strandtmann and Morlan 1953). All other mites from northern flying squirrels constitute new host records.

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Medicine, University of Washington, Seattle, Washington), Gerald W. Krantz (Department of Entomology, Oregon State University, Corvallis, Oregon), and Robert E. Lewis reviewed the manuscript.

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Eight Range Extensions for the Alaska Flora

Abstract

A floristic survey of the Cinnabar Creek area of the Kuskokwim District of Alaska revealed eight species previously unknown to the area: *Arabis arenicola* (Richards.) Gelert, *Fragaria virginiana* Duchesne, *Galium triflorum* Michx., *Geum macrophyllum* Willd., *Parnassia fimbriata* Konig, *Phleum commutatum* Gandoger, *Rumex crispus* L., and *Trichophorum alpinum* (L.) Pers. Searches of the literature and herbaria with significant Alaskan collections confirmed the range extensions of 200-640 km for the eight species. Four specimens apparently represent the westernmost collections in North America.

Introduction

Numerous botanical collections have been made in Alaska in the last 200 years, but due to the size of the state and the relative inaccessibility of many areas, the ranges of many species are still incompletely known (Hulten 1968). The lower Kuskokwim River area between the Yukon River and the Wood River Lakes region is one of the least botanically known (D. F. Murray, University of Alaska, pers. comm.). A floristic survey of a localized area in this region revealed range extensions of eight species.

Methods

The observations reported herein are the result of a botanical survey conducted around the Cinnabar Creek area, T8N R54-55W (Seward Meridian) in the Kuskokwim District of southwestern Alaska (Fig. 1). A search of the literature published since the publication of Hulten's (1968) Flora of Alaska was made to substantiate the reported range extensions. Herbaria with substantial Alaskan plant collections were also consulted: State Museum of Natural History (Riksmuseum), Stockholm—S; Gray Herbarium—GH; U.S. National Herbarium—US; National Herbarium of Canada—CAN; University of British Columbia—UBC; and University of Alaska at Fairbanks—ALA.

Voucher specimens have been deposited at the Emory University Herbarium (GEO). Nomenclature follows Hulten (1968).

Range Extensions

Arabis arenicola (Richards.) Gelert (Brassicaceae). Kuskokwim District: T8N R55W (Seward Meridian) Section 12, near ore (cinnabar) dump at Princess mine, stream side, 400 m, 29 August 1980, Phillips 208. Associated species: *Juncus castaneus*, *Carex* spp. Range extension: 300 km SSE of the previous southernmost Alaskan record (Hulten 1968).

Fragaria virginiana Duchesne subsp. *glauca* (S. Wats.) Standt (Rosaceae). Kuskokwim District: T8N R55W (Seward Meridian) Section 12, 0.5 km east of Cinnabar Creek

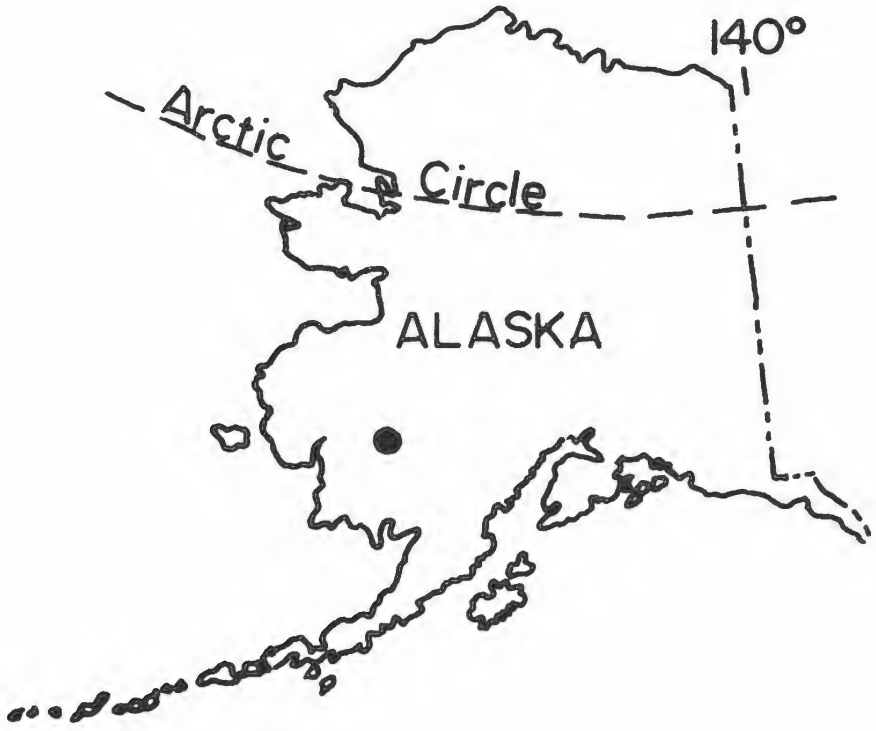

Figure 1. Location of the study site (black dot).

on road to Princess mine, roadside, 365 m, 4 September 1980, Phillips 224. Associated species: *Cornus canadensis*, *Alnus tenuifolia, Salix* sp. Range extension: 640 km SW of a collection originally labelled *F. yukonensis*, 5 July, 1941, J. P. Anderson 7094 (CAN), which was taken at Manly Hot Springs. This extension represents the new westernmost point of ranges of both subsp. *glauca* and the species as a whole.

Galium triflorum Michx. (Rubiaceae). Kuskokwim District: T8N R55W (Seward Meridian) Section 12, 0.2 km northeast of Princess mine, alder thicket, 450 m, 4 September 1980, Phillips 223. Associated species: *Alnus tenuifolia.* Range extension: approximately 280 km to the northwest from the previously known range (Hulten 1968).

Geum macrophyllum Willd. subsp. *perincisum* (Rydb.) Hult. (Rosaceae). Kuskokwim District: T8N R55W (Seward Meridian) Section 12, near ore (cinnabar) dump at Princes mine, stream side, 400 m, 29 August 1980, Phillips 210. Associated species: *Juncus castaneus, Carex* spp. Range extension: approximately 200 km S of the nearest collection shown by Hulten (1968) and 200 km SW of another collection along the Kuskokwim River—14 July, 1949, W. H. Drury 1978 (CAN).

Parnassia fimbriata Konig (Saxifragaceae). Kuskokwim District: T8N R55W (Seward Meridian) Section 12, 0.5 km W of Princess mine, wet lowlands, 365 m, 4 September

1980, Phillips 215. Associated species: *Sphagnum* sp., *Carex* spp., *Vaccinium uliginosum, Betula nana, Potentilla fruticosa, Trichophorum alpinum.* Range extension: approximately 340 km SW of the previous westernmost record (Drury 2858 (CAN); 12 August, 1949; Farewell, Alaska; 62° 31′N, 153° 53′W). This record represents the new westernmost locality for the species.

Phleum comutatum Gandoger (Poaceae). Kuskokwim District: T8N R55W (Seward Meridian) Section 13, 0.5 km N of mine camp, roadside, 335 m, 5 September 1980, Phillips 229. Associated species: *Alnus tenuifolia, Salix barclayi.* Range extension: approximately 300 km WNW from the base of the Alaska Peninsula where several collections have been made (Hulten 1968).

Rumex crispus L. (Polygonaceae). Kuskokwim District: T8N R55W (Seward Meridian) Section 13, at mine camp, disturbed areas around buildings and airstrip, 335 m, 6 September 1980, Phillips 235. Associated species: *Epilobium angustifolium.* Range extension: 500 km NW of the closest of several widely scattered Alaskan collections (Raspberry Island in the Kodiak group; Eyerdam 3794 (CAN), 8-10 July, 1945). This report is the new westernmost record for North America.

Trichophorum alpinum (L.) Pers. (Cyperaceae). Kuskokwim District: T8N R55W (Seward Meridian) Section 12, 0.5 km W of Princess mine, wet lowlands, 365 m, 4 September 1980, Phillips 216. Associated species: *Sphagnum* sp., *Carex* spp., *Vaccinium uliginosum, Betula nana, Potentilla fruticosa.* Range extension: about 300 km SW from the range reported in Hulten (1968), representing the westernmost record for the species in North America.

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Grizzly Bears in Idaho's Selkirk Mountains: an Update

Abstract

A grizzly bear (*Ursus arctos horribilis* L.) survey was conducted in north Idaho's Selkirk Mountains in 1981. This survey updates and supplements Layser's (1978) work. Fifty-nine reliable accounts of grizzly bear sightings or evidence since 1975 are reported. The Selkirks, in conjunction with the Salmo River area, the Purcell and West Cabinet mountains, and southern British Columbia appear to provide adequate suitable habitat to support a viable grizzly bear population.

Introduction

The grizzly bear was classified as a "threatened species" (Endangered Species Act 1973) in the contiguous United States in 1975. This classification resulted from a substantial population decline since the arrival of European man in the western U.S. Today, grizzly bears in the lower 48 states are restricted to the Yellowstone National Park area and the northern Rocky Mountains of Montana, Idaho, and northwest Washington (USFWS 1981).

Relatively little was known about grizzly bears in the U.S. until 20 years ago. An intensive study of grizzly bear ecology was conducted in Yellowstone National Park during the 1960s (Craighead and Craighead 1972a, 1972b). More recently, research was conducted by the Interagency Grizzly Bear Study Team in Yellowstone National Park (Judd and Knight 1980). Martinka (1974a, 1974b, 1976) reported on bears in Glacier National Park. In 1975, the U.S. Fish and Wildlife Service and the Montana Department of Fish, Wildlife and Parks initiated grizzly bear research in northwestern Montana. That work included studies of the distribution and productivity of huckleberry (*Vaccinium* spp.), a major bear food (Martin 1979); the role of logging and wildfire on grizzly bear habitat (Zager 1980); and grizzly bear ecology in the Mission Mountains (Servheen 1981).

Excepting Layser's (1978) summary of the historical distribution of grizzly bears in the Selkirks, grizzly bear information is lacking for the Selkirk and Purcell mountains in Idaho, the Salmo Mountains in northeast Washington, and the Cabinet Mountains in northwest Montana. The overall goal of this survey was to collect preliminary information on grizzly bear distribution and habitat suitability in the Selkirk Mountains. More specific objectives included:

(1) summarizing recent records of grizzly bear observations and evidence to supplement and update Layser's (1978) work; (2) describing grizzly bear habitat use in the Selkirks by documenting feeding sites, scats, tracks, and other indirect evidence; and (3) assessing suitability of the area for grizzly bears.

This survey focused on that portion of the Selkirk Mountains in the northwest corner of Idaho's panhandle. This area corresponds roughly with currently occupied grizzly bear range (USFWS 1981). Elevations range from 750 m to over 2250 m. The

topography is rugged with exposed bedrock common at mid-to-high elevations. The Pacific maritime influence dominates the area, resulting in normally long, snowy winters and short, damp summers.

The forests are dominated by western hemlock (*Tsuga heterophylla*) and subalpine fir (*Abies lasiocarpa*) which are potential climax series (Daubenmire and Daubenmire 1968), though pockets of Douglas-fir (*Pseudotsuga menziesii*) and western red cedar (*Thuja plicata*) series are also found. Shrubfields and both mesic and dry meadows are interspersed throughout the forest, creating a diverse mosaic of plant communities across the landscape.

Historically, wildfire was a significant factor affecting the Selkirk landscape. The past 50 years of effective fire suppression have reduced this influence. The most recent major wildfires in the area were the 6000 ha Trapper Peak Fire and the 9000 ha Sundance Fire, both in 1967. Currently, timber harvest and associated activities are the most important influences on vegetation and wildfire of the area. Though some commercial logging was done as early as the 1920s, most activity on the survey area dates from the 1960s. Approximately 8000 ha of the survey area and adjacent Washington are included in the proposed Salmo-Priest Wilderness Area (Fig. 1).

Methods

Records from the following were searched for recent (since 1975), reliable grizzly bear accounts: (1) the Border Grizzly Project (BGP) at the University of Montana; (2) the Bonner's Ferry Ranger District, Idaho Panhandle National Forests; (3) the

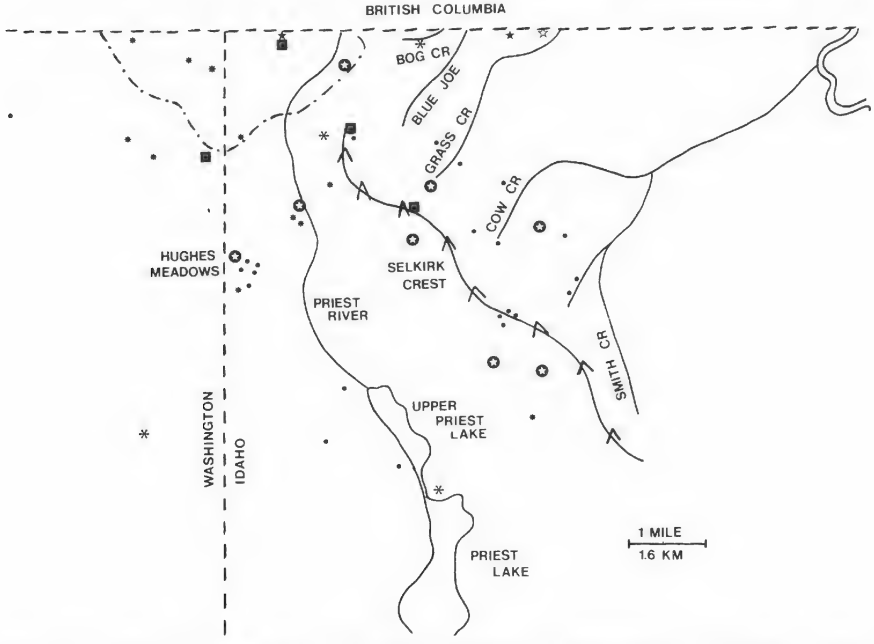

Figure 1. Evidence of grizzly bears in the Selkirk Mountains, northern Idaho, 1975-1981. 1975 *; 1976 ★; 1977 ■; 1978 ☆; 1979 ✪ ; 1980 ∗ ; 1981 •; proposed Salmo-Priest Wilderness Area —·—·—

Priest Lake Ranger District, Idaho Panhandle National Forests; and (4) the Idaho Department of Fish and Game. To supplement and update these records, people knowledgeable about bears and/or the Upper Priest River area were interviewed. The validity of each record was rated according to a somewhat subjective 1-5 scale. A report of grizzly bear sign or a sighting that was confirmed or verified by someone knowledgeable about bears was given a "5" rating. There was no reason to doubt the veracity of an account that received this rating. A rating of "4" was assigned to records that were probably valid based on the reporter's bear experience and the type of evidence. Scats were often rated 4 because of the potential for classification error resulting from size overlap between black bear and grizzly bear scats, even though conservative criteria were used (see below). Accounts that were possibly valid received a "3" rating. A sketchy observation report by an inexperienced observer would be rated no higher than 3. Accounts that were weaker than 3 were not considered valid. Records were coded by year and plotted on a ½":1 mile map (Fig. 1).

Extensive ground reconnaissance and a fixed-wing aircraft flight were conducted in areas of repeated grizzly bear accounts and other areas of apparently suitable habitat between 11 June and 7 August 1981. In addition, a search for grizzly bear dens was conducted by helicopter (Servheen 1981) on 5 August. Evidence of grizzly bear use of areas searched during the ground reconnaissance was recorded. Discernible evidence included tracks, scats, excavations for rodents, logs torn apart for insects, and overturned rocks. Tracks were considered to be those of grizzly bears if the claw marks were at least 3.8 cm in front of the toe pads. Scats greater than 5 cm in diameter and/or with a volume greater than 1.0 liter were classified as grizzly bear scats. These criteria are conservative (Hamer *et al.* 1981), thereby minimizing classification error. Pertinent information regarding the communities occupying these sites such as the abundance of important grizzly bear foods, phenological stage of the vegetation, and site accessibility were also recorded.

Results and Discussion

Past Grizzly Bear Reports

The evidence of grizzly bears reported since 1975 in Idaho's Selkirk Mountains is summarized in Table 1 and Figure 1. Most recent evidence of grizzly bear activity occurs north of Upper Priest Lake. Reports south of the lake are infrequent. There are several possible explanations for this pattern:

1. The Priest Lake area is gaining popularity as a summer resort area. Land is being developed for summer and year-around homes and the number of tourists is rapidly increasing. Moderate to high levels of human activity can displace wildlife populations, including grizzly bears, as a result of both direct and indirect conflicts.

2. The level of resource management, particularly timber harvest and associated activities, is much greater south of Upper Priest Lake than it is north of the lake. This habitat alteration could modify the habitat in such a way that it is no longer suitable for grizzly bears by removing favored food items and security cover, altering traditional travel routes, or introducing a disturbance factor in the form of increasing human activity. Poaching could also be a significant problem in areas where there is ready access.

3. Another possibility is that the habitat south of Upper Priest Lake, even under pristine conditions, is not suitable to support bears. Some support for this hypothesis

TABLE 1. Grizzly bear accounts for the Selkirk Mountains of northeastern Washington, northern Idaho, and adjacent Montana (1975-1981).

Date	Observer	Source	Account	State	Location	Comments
1975 1975	Greene	Pers. Comm.	Tracks[1]	ID	Lookout Lake T63N R3W S6	Spring—tracks in mud and snow. Hind track large enough to place Size 13 boot into.
1975	Caswell	Burke	Tracks	WA	S. Fk. Currant Cr. T38N R42E S6	
1975		Border Grizzly Project (BGP)	Sighting of female and 2 cubs	ID	T64N R5W S15	
1975		BGP	Tracks	WA	T40S R45E S5	
1975		BGP	Track	WA	N. Baldy Mtn. T35N R45E S8	
1975	Caswell	Burke	Tracks	WA	Deemer Cr. T40N R45E S34	
1975		Burke	Tracks	WA	S. Fork Salmo River T40N R45E S12	
1975		BGP	Tracks	WA	Leola Peak T40N R45E S28	
1975	Lyon	BGP	Tracks	ID	Snowy Top Trail T65N R5W S32	
1975	Kitts	BGP	Tracks	MT	N. Fork 17 Mile Cr. T34N R32W S33	
1975		Carrier	Sighting of 2 females and cubs	ID	Lime Creek T64N R5W S11	
1975		Keniston	Track	WA	S. Fork Salmo River T40N R45E S11	
1975	Greenley	BGP	Observation	ID	Priest Lake T64N R5W S15	
1975	Lyons	BGP	Tracks	ID	Trail 311, west of Hughes Meadows T64N R5W S32	
1975	Bennett	BGP	Sighting of female and 2 cubs	ID	Lost Creek T62N R1W S4	
1976 (Aug.)	Mealey and Jonkel	BGP	Scat[1]	ID	Snowy Top T65N R5W S9	**Osmorhiza** sp. and **Angelica** sp.
1976	Lohman	BGP	Observed	ID	Grass Creek T64N R4W S12	

TABLE 1. (Continued)

1976	Haney	BGP	Track	MT	N. Fork 17 Mile Cr. T34S R32W S28	
1977 (June)	Servheen	BGP	Scat	MT	W. Fork Yaak River T65S R33W S32	2¼ inch dia.
1977 (Aug.)		Summerfield	Observed 1 bear	ID	Beehive Lake T61N R2W S6	
1977 (Aug.)		Summerfield	Observed 1 bear	ID	Hunt Creek T60N R3W S3	
1978 (May)	Lohman	Pers. Comm.	Observed 2 bears and tracks	ID	Grass Creek T65N R3W S7	Hind track 11¾ inches long and 5¼ inches wide.
1978 (June)		Summerfield	Observed 1 bear	ID	T61N R2W S16	
1978	Douglas	Hawn	Observed 1 bear	ID	S. End of Priest Lake T59N R4W S ?	Bear repeatedly visited a cow carcass.
1979 (Spring)		BGP	Observation	ID	Hughes Meadow T64N R5W S29	
1979 (Spring)	Cook	Pers. Comm.	Tracks	ID	T65N R5W S24	
1979 (June)	McCrea	Summerfield	Tracks	ID	T64N R4W S9	Cast taken
1979	Low	Pers. Comm	Observed 1 bear	ID	Abandon Creek T63N R3W S18	Stopped to look at tracks in road when he saw the bear.
1979 (Aug.)	Beecham	BGP	Track	ID	Bugle Creek T63N R4W S14	Track was 6-7 inches wide.
1979 (Aug.)	Their	BGP	Scat, digs	ID	Joe Lake T64N R3W S19	Found in alpine meadow.
1979 (Sept.)	Weatherman	Burke and BGP	Kill	WA	W Branch LeClerc Cr. T36N R44E S7	Hunter mistook grizzly for a black bear.
1979 (Oct.)	Donahoe	Pers. Comm	Observation	ID	Trapper Peak T64N R4W S20	Small to medium sized grizzly traveling through Trapper Burn.
1979 (Nov.)	Miller	Pers. Comm	Tracks	ID	Upper Priest River T64N R5W S15	Tracks 7 inches wide; claws distinctive. Bear was on white-tail deer carcass.
1980 (May)	Carrier	BGP	Digs	ID	Parker Creek T64N R1W S8	Possibly digging for glacier lily or spring beauty.
1980 (July)	Zender	Burke	Tracks	WA	Willow Creek T38S R45E S21	

TABLE 1. (Continued)

1980 (June)	Zender, VanSkyock, Higginbothum	Burke	Tracks	WA	Middle Branch of LeClerc Cr. T36S R44W S10	Photo and cast taken.
1980	VanSkyock, Higginbothum	Burke	Observation	WA	Harvey Creek T38N R44E S27	
1980	Neff	Pers. Comm.	Tracks	ID	Bog Creek T65N R4W S8 or 9	Track 11-12 inches long with claw marks well out in front of pads.
1980 (June)	Donahoe	Pers. Comm.	Tracks	ID	T62N R4W S4	
1981 (April)	Wheeler	Pers. Comm.	Den	ID	Cow Creek T64N R4W S12	Observed cavity 200 feet from ridge. Dirty snow piled in front.
1981 (May)	Horn and Higginbothum	Burke	Tracks	WA	T40N R44E S23	Front print 6 inches wide by 9 inches long.
1981 (May)	Beecham	Pers. Comm.	Observed 1 bear	ID	Between S. Fork of Indian Cr. and Horton Cr. T61N R4W S25	Feeding on Dandelions along the road.
1981 (June)	Bourassa, Lohman, Gerhart		Observed 1 grizzly	ID	Grass Creek T64N R4W S3	Bear seen in forest at edge of clearcut.
1981 (June)	Jerry		Scat	ID	Hughes Meadow T64N R5W S29	Found in timber bordering meadow.
1981 (June)	Garner		Scat	ID	Hughes Meadow T64N R5W S29	Found in patch of cow parsnip in meadow.
1981 (June)	Zager		Scat	ID	Hughes Meadow T64N R5W S29	Found in timber bordering meadow.
1981 (June)	Zager		Scat	ID	Bugle Ridge T63N R4W S1	Found on ridgetop snowbank.
1981 (June)	Garner		Scat	ID	Bugle Ridge T63N R4W S1	
1981 (June)	Garner		Scat	ID	Bugle Ridge T63N R4W S1	
1981 (June)	Garner		Scat	ID	Bugle Creek T63S R4W S1	
1981 (June)	Richardson	Pers. Comm.	Scats	ID	Plowboy Trail T62N R4W S5 T62N R4W S35 T62N R4W S24	3 scats along trail.

TABLE 1. (Continued)

1981 (June)	Garner		Scat	ID	Hughes Meadow T64N R5W S9	
1981 (July)	Zager		Scat	ID	West Fork Lake Trail T64N R4W S33	
1981 (July)	Zager		Scat	ID	West Fork Lake Trail T64N R4W S33	
1981 (July)	Zager		Scat	ID	Phoebe Basin T64S R4W S23	
1981 (July)	Zager		Tracks	ID	Cow Creek T64S R4W S23	
1981 (July)	Clark	Pers. Comm.	Scat	ID	Hughes Meadow T64N R5W S29	
1981 (July)	Zager and Garner		Digs	ID	Continental Mountain T65N R5W S36	Extensive digs for columbian ground squirrels.
1981 (Sept.)	Carr	Beecham	Observed 1 bear	ID	Grass Mountain T65N R4W S33	Observed bear at 80 yards.

[1]Only tracks and scats that meet the criteria described under **Methods and Materials** are included in this summary.

comes from Layser's (1978) data. His report included few grizzly bear locations south of the upper lake since 1900, prior to significant increase in human activity and resource management. Typical suitable grizzly bear habitat in the northern Rocky Mountains consists of a mosaic of plant community types, especially naturally open communities (tree canopy $<$ 30 percent), such as wet meadows and wildfire-induced shrubfields (Herrero 1978, Zager 1980, Servheen 1981). Such naturally open areas are common along the Selkirk Crest and north of Upper Priest Lake; they are much less frequent south of the lake.

Perhaps this historic pattern of grizzly bear reports results from a combination of these and other factors.

Field Reconnaissance Evidence

Field reconnaissance resulted in the identification of several areas used extensively by grizzly bears. Five large bear scats (presumably grizzly bear scats) were collected in late June from the timbered margin of Hughes Meadow (a low elevation wet meadow). Analysis revealed the bear(s) fed primarily on sedges (*Carex* spp.) and cow parsnip (*Heracleum lanatum*) in the meadow (Table 2). Analysis of 7 other spring grizzly bear scats indicated that ungulates (probably deer) and various forbs were also consumed. No scats were found that would indicate summer or fall food habits.

Excavations for Columbian ground squirrels (*Spermophilus columbianus*) were found on Continental Mountain and Snowy Top. Digs for glacier lily (*Erythronium grandiflorum*) were found throughout the area. Rocks, overturned by bears in search of insects, were found on Snowy Top, Bugle Ridge, and in other areas. Grizzly bear tracks were found on an old fire road at the head of Cow Creek.

Constituent Elements

The constituent elements of grizzly bear habitat as defined by the USDA Forest Service (1981) include 1) spring range, 2) summer range, 3) fall range, 4) denning habitat, and 5) space and solitude. Requirements for these constituent elements must be met for a grizzly bear population to survive in an area.

Spring range includes areas that are snowfree and produce an abundance of succulent vegetation early in spring. Ungulate winter range where carrion may be present is also included. In the Selkirks, spring range is provided by the following habitat components: (1) south-facing snowchutes that are found, for example, on Shedroof Mountain and Snowy Top (see Fig. 1); (2) low elevation wet meadows such as Hughes Meadows and certain areas along Bog Creek, Cow Creek, and Grass Creek; and (3) the closed-canopy bottomland forest along the Upper Priest River.

Summer grizzly bear habitat includes areas that remain relatively moist and produce succulent vegetation throughout the summer, and components that provide "early" berries, or starchy roots and tubers. Summer grizzly bear habitat requirements are satisfied by the following components: (1) high elevation wet meadows such as those at the heads of Cow, Trapper, and Grass creeks; (2) creekbottom shrubfields found throughout the area; (3) meadows at the heads of snowchutes such as those on Snowy Top; and (4) meadows on dry, steep sites such as those on Continental Mountain and Hughes Ridge.

TABLE 2. Contents of grizzly bear scats collected in the Selkirk Mountains, 1981.

Date collected	Location	Elevation	Contents	Percent composition	Remarks
22 June	Hughes Meadows	790 m	**Heracleum lanatum**	99	Collected in **Heracleum lanatum** patch
	T64N R5W S29	2620 ft	Debris	1	in meadow.
22 June	Hughes Meadows	790 m	Graminoids	90	Collected along timbered margin of
	T64N R5W S29	2620 ft	**Heracleum lanatum**	10	meadow.
22 June	Hughes Meadows	790 m	Graminoids	95	Collected along timbered margin of
	T64N R5W S29	2630 ft	Debris	5	meadow.
23 June	Bugle Creek	1600 m	Graminoids	40	Grassy area intermixed with patches of
	T63N R4W S1	5300 ft	**Vaccinium** sp. flowers/ leaves	50	**Alnus sinuata** and **Vaccinium** sp.
			Heracelum lanatum	10	
23 June	Bugle Creek	1600 m	Graminoids	70	Rock slab near patch of **Sorbus**
	T63N R4W S1	5300 ft	**Vaccinium** sp. flowers/leaves	20	**scopulina, Alnus sinuata**, and
			Unidentified forb	10	**Vaccinium** sp.
23 June	Bugle Creek	1600 m	Graminoids	60	Patch of **Sorbus scopulina, Alnus**
	T63N R4W S1	5300 ft	**Vaccinium** sp. flowers/leaves	40	**sinuata**, and **Vaccinium** sp.
23 June	Bugle Creek	1600 m	Graminoids	100	Collected on snowfield on the
	T63N R4W S1	6400 ft			ridgetop.
29 June	Hughes Meadows	790 m	Graminoids	95	Collected in timber bordering the
	T64N R5W S29	2620 ft	Unidentified forb	1	meadow.
			Debris	4	
2 July	Smith Creek	1450 m	**Odocoileus sp.**	99	Along trail to West Fork Lake.
	T64N R3W S32	4800 ft	Graminoids	1	
2 July	Smith Creek	1450 m	Graminoids	90	Along trail to West Fork Lake.
	T64N R3W S32	4800 ft	Unidentified forb	10	
4 July	Cow Creek	1640 m	Graminoids	95	Wet meadows in basin at head of Cow
	T64N R4W S23	5400 ft	Unidentified forb	4	Creek.
			Debris	1	
8 July	Hughes Meadows	790 m	**Heracleum lanatum**	95	Near timbered border of the meadow.
	T64N R5W S29	2620 ft	Graminoids	5	

Grizzly bears feed on berries (e.g., huckleberries; mountain ash, *Sorbus* spp.; serviceberries (*Amelanchier alnifolia*)), often to the near exclusion of other food items, during the fall. Therefore, fall grizzly bear habitat includes components in which berries are abundant. During poor berry years, creekbottoms and high elevation wet meadows remain important throughout the fall. The following habitat components satisfy, in large part, fall grizzly bear habitat requirements in the Selkirks: (1) wildfire-induced shrubfields such as those created by the Trapper Peak and Sundance fires; (2) shrubfields in certain cutting units (unscarified sites at least 10 years old); (3) shrubfields on dry, steep sites that are scattered throughout the area; (4) high elevation wet meadows; and (5) creekbottom shrubfields.

Denning habitat is also available in the Selkirks. Several probable dens were discovered during the helicopter survey. They were located on a steep, southwest slope northwest of Snowy Top. The area was a dry meadow with scattered timber and shrubs. Though no other dens were found, habitat very similar to known grizzly bear denning habitat in the Mission Mountains (Servheen 1981, pers. comm.) and the Flathead National Forest was found at high elevations in the drainage heads along the Selkirk Crest. Layser's (1978) report mentioned a possible denning area at the head of the West Fork of Smith Creek. After inspecting the area, I concur that the Smith Creek area appears to be suitable denning habitat.

Space and solitude are nebulous qualities of grizzly bear habitat that are extremely difficult to quantify. The minimum viable grizzly bear population size is 30-70 bears (Shaffer 1978). Because the average grizzly bear density in the northern Rocky Mountains is 1 bear per 50 sq. km. (USFWS 1981), 1500-3500 sq. km. of contiguous suitable habitat is needed to support a minimum viable population. There are only 1108 sq. km. of occupied, and presumably suitable, grizzly bear habitat in Idaho's Selkirk Mountains (USFWS 1981). But the Selkirk grizzly bears do not represent a completely isolated population. The adjacent proposed Salmo-Priest Wilderness Area and adjacent lands in British Columbia combine with the Selkirks to provide ample habitat to meet the space requirements for a viable population.

In summary, based on this reconnaissance survey, I believe all the elements of grizzly bear habitat are provided in the northern part of the Selkirk Mountains of Idaho. Even though Selkirk grizzly bears represent a fringe population at the edge of occupied range, the area is contiguous with adjacent areas of suitable habitat. These areas complement one another, creating an area that is suitable for a viable population of grizzly bears. The potential for survival of the Selkirk grizzly bear population depends on the management direction taken by the appropriate land and wildlife management agencies in the U.S. and Canada, and the successful implementation of Grizzly Bear Recovery Plan.

Acknowledgments

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New Distributional Records of Ticks (Ornithodoros concanensis and O. kelleyi) in Washington

Abstract

Nymphs of *Ornithodoros concanensis* and larvae of *O. kelleyi* were collected from a Golden Eagle (*Aquila chrysaetos*) nest and from pallid bats (*Antrozous pallidus*), respectively. Both species of ticks were previously unreported for Washington.

On 22 May 1980, seven nymphs of *Ornithodoros concanensis* were collected from a rock flake 15 cm above an active Golden Eagle nest. That nest, which fledged one young, was located 12 m up in a 18 m high basalt cliff in Klickitat County, Washington. *O. concanensis* (previously confused with *O. aquilae*; see Kohls *et al.* 1965) was first described from specimens found on bat guano and has subsequently been reported from swallows and raptorial birds (Kohls *et al.* 1965) in several western states though, until now, was previously unrecorded in Washington.

On 9 August 1980, 10 larvae of *O. kelleyi* were collected from four live pallid bats (3 females, 1 male; *Antrozous pallidus*) captured in a rock crevice on a granite cliff in Douglas County, Washington. Over a dozen bats, all apparently *A. pallidus*, were roosting in the crevice. This species of tick has been collected only from bats and bat-inhabited structures. The species is widely distributed in the United States and, until now, was previously unrecorded in Washington.

All specimens of both *O. concanensis* and *O. kelleyi* were identified by Carleton Clifford and are retained in the collection of the Rocky Mountain Laboratory (RML 113340 and RML 113341, respectively), National Institutes of Health, Hamilton, Montana. The four specimens of *A. pallidus* are retained in the University of Washington, Washington State Museum (UW-WSM 32505-32508), Seattle, Washington.

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Association News

Annual Meeting

The 56th Annual Meeting of the Northwest Scientific Association was held at The Evergreen State College on 24-26 March. The meeting included a symposium on the Ecological Recovery at Mount St. Helens. The Association had the pleasure of an excellent and informative banquet speech by Dan Evans, President of The Evergreen State College, on the "Northwest Power Planning Council Decision-making Process." The General Chairman of the meeting was John Perkins. Alfred M. Wiedemann of The Evergreen State College was Program Chairman.

Two hundred papers were presented in the following symposium sections: Botany, Forestry, Geology, Physical Sciences, Science Education, Soil and Water, and Zoology. Copies of the Program and Abstracts are out of print and no longer available.

Richard Naskali, Associate Professor of Botany, University of Idaho, was named an Honorary Life Member by the Association in recognition of his many years of service to the Association, especially as Treasurer. Research grants totaling $1797 were awarded to: Robert R. Blank, University of Idaho; John A. Christy, University of British Columbia; Matthew H. Dick, Western Washington University; N. R. Emerson *et al.*, Eastern Washington University; John Henkins, Washington State University; Diana Kimberling, Oregon State University; Lyndon C. Lee, University of Washington; and Lori Terwilliger, Washington State University.

The new officers of the Association are: President, Stephen F. Arno; Vice-President, Oscar Sziklai; and Treasurer, Steven J. Brunsfeld. Five new Trustees were elected to the Board: Donald Hanley, Warren Illiff, Susan Kephart, Robert Stockhouse, and B. J. Verts.

1984 Annual Meeting

The meeting dates for the 1984 Annual Meeting of the Association at the University of Montana are 21-24 March.

Treasurer's Report (1982)

Income	$14,340.91
Expenses	$14,430.37
Checking Balance, Dec. 31	$ 8,595.94
Reserve Fund, Dec. 31	$ 4,000.00
Research Fund, Dec. 31	$10,000.00

Editor's Report (1982)

Forty-six papers were published in Volume 56 of *Northwest Science*. Of 50 new manuscripts received, 35 were accepted for publication.

Shrub Research Consortium Formed

The Forest Service's Intermountain Forest and Range Experiment Station, the Utah Division of Wildlife Resources, Brigham Young University, and Utah State University announce the formation of a Shrub Research Consortium. Formed to promote, support, and coordinate programs of research and associated graduate education, the Consortium will be located at the Shrub Sciences Laboratory, 735 North 500 East, Provo, Utah 84601. Activities will relate to: (1) improvement and development of shrub plant materials; (2) methods of seeding, planting, culture, and management of shrubs in natural settings; and (3) assistance where feasible with publishing and disseminating research results.

Specific goals of the Consortium are:

1. Develop a program consisting of statements of research needs and priorities and current studies aimed at meeting those needs. The Consortium may determine and set objectives, priorities, and guidelines for studies, based on interpretation of need, available funds, capabilities of institutions and personnel, and other work under way within or outside the Consortium. Principal areas of shrub research will include, but will not be limited to: ecology, genetics, pathology, entomology, soils, hydrology, wildlife habitat, and livestock grazing.

2. Encourage proposals to conduct research from both member and nonmember institutions desiring to participate and capable of contributing appropriately to solving problems selected for study.

3. Arrange for printing and distribution of publications and reports.

4. Sponsor seminars, conferences, symposia, and other meetings to coordinate research on wildland shrubs and to disseminate research results.

Applications for membership from organizations involved in wildland shrub research are encouraged.

For further information contact:

Dr. Arthur R. Tiedemann, Chairman SRC
Shrub Sciences Laboratory
Intermountain Forest and Range Experiment Station
735 N. 500 E.
Provo, Utah 84601

Meetings

The Cooper Ornithological Society (COS) will hold its 54th annual meeting at Humboldt State University, Arcata, California, 19-22 June 1984, preceding the annual meeting of the American Society of Mammalogists (24-28 June) at the same location. The COS will include a variety of events (pelagic birdwatching, rafting on local rivers, and tours of Redwood National Park) in addition to the scientific program.

Northwest Science Index (1973-82)

A cumulative author bibliography and subject index for *Northwest Science* for the years 1973-82 is available from the Treasurer. Cost per copy:

$5 for individual members;

$10 for non-institutional members and non-sustaining members.

The Treasurer will mail (free of charge and without request) single copies of the index to sustaining individual members, sustaining institutional members, and institutional members.

Northwest Science

Volume 57, 1983

John W. Weber, Editor

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At least one of the authors of all papers considered for publication must be a member of the Northwest Scientific Association.

Manuscripts—Submit three copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten on 8½x11 paper and *double-spaced throughout (including abstract, acknowledgments, literature cited, tables, and legends for figures)*; provide ample margins. Computer printouts are not acceptable. Avoid unnecessary footnotes. Do not break words at the end of a line. Format and style of manuscripts should conform to general usage in recent issues.

An abstract, double-spaced and not exceeding five percent of the paper, should precede every article. The abstract should recapitulate the major points of the paper and should be suitable for use by abstracting services.

Literature citations should have the author's name and year of publication in the text; e.g. (Jones 1978). Citations should be double-spaced and listed in alphabetical order at the end of the article.

Present all data in international (SI) units. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2230) and continental dating (17 November 1982).

Equations should be presented camera-ready. Symbols should be large enough to be legible after a ⅓ to ½ reduction in size, but not overly large.

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